THE NEURAL DEVELOPMENT OF VISUOHAPTIC OBJECT PROCESSING

Ruth Joanne Jao

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Doctoral Committee

_____

Thomas W. James, Ph.D., Co-chair

_____

Karin H. James, Ph.D., Co-chair

_____

Sharlene Newman, Ph.D.

_____

Dan Kennedy, Ph.D.

May 1, 2015

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Coauthorship

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Ruth Joanne Jao

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Object recognition is ubiquitous and essential for interacting with, as well as learning about, the surrounding multisensory environment. The inputs from multiple sensory modalities converge quickly and efficiently to guide this interaction. Vision and haptics are two modalities in particular that offer redundant and complementary information regarding the geometrical (i.e., shape) properties of objects for recognition and perception. While the systems supporting visuohaptic object recognition in the brain, including the lateral occipital complex (LOC) and the intraparietal sulcus (IPS), are well-studied in adults, there is currently a paucity of research surrounding the neural development of visuohaptic processing in children. Little is known about how and when vision converges with haptics for object recognition. In this dissertation, I investigate the development of neural mechanisms involved in multisensory processing. Using functional magnetic resonance imaging (fMRI) and general psychophysiological interaction (gPPI) methods of functional connectivity analysis in children (4 to 5.5 years, 7 to 8.5 years) and adults, I examine the developmental changes of the brain regions underlying the convergence of visual and haptic object perception, the neural substrates supporting crossmodal processing, and the interactions and functional connections between visuohaptic systems and other neural regions. Results suggest that the complexity of sensory inputs impacts the development of neural substrates. The more complicated forms of multisensory and crossmodal object processing show protracted developmental trajectories as compared to the processing of simple, unimodal shapes. Additionally, the functional connections between visuohaptic areas weaken over time,

which may facilitate the fine-tuning of other perceptual systems that occur later in development. Overall, the findings indicate that multisensory object recognition cannot be described as a unitary process. Rather, it is comprised of several distinct sub-processes that follow different developmental timelines throughout childhood and into adulthood.

Keywords: Multisensory; Vision; Haptics; Object recognition; Crossmodal; Development; Functional connectivity; fMRI; gPPI.

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Thomas W. James, Ph.D., Co-chair

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Karin H. James, Ph.D., Co-chair

_____

Sharlene Newman, Ph.D.

_____

Dan Kennedy, Ph.D.

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Chapter 1.

General Introduction

1.1. Preamble

Object recognition is a robust phenomenon that is intrinsically multisensory in the real world. Information about objects in the environment can be acquired from multiple senses, in particular, vision and touch. Both the visual and haptic systems provide rich details about an object, and are also complementary with regard to the types of information, such as shape, used to represent and recognize that object. As such, object recognition is most benefited by the integration of multisensory inputs (Rentschler et al., 2004). Interactions between the different sensory modalities, particularly vision and haptics, form the basis of our experiences with an inherently multisensory environment. As adults, we are able to move around in, interact with, and perceive our surroundings quickly and efficiently. To do so requires the ability to recognize the objects within that environment and to act on them accordingly. This is facilitated by sensorimotor processes that integrate information from multiple systems in the brain. These sensorimotor systems are involved in a perception and action system, in a feedback and feed forward loop, that is vital for interacting with, as well as learning about, the environment and the objects within it.

Generally, the concept of sensorimotor processing has been divided into sensory components and motor components. While the former consists of perceptual skills, which are deemed the most basic of sensorimotor processing and include visual and haptic perception, the latter is comprised of actions, which refer to the performative aspect of

sensorimotor processing and include behaviors (i.e., motor movements) from looking to reaching and grasping to haptic manipulation (Affolter, 2004). These perceptual and performative abilities are inextricably linked to one another, and allow for multisensory visuohaptic object recognition to occur.

While the visual and haptic systems supporting object recognition are well-researched in adults, they are not so in children; there have been few developmental studies examining the neural correlates of haptic or visuohaptic processing. Yet, to fully understand multisensory object recognition, we must turn to development and examine the progression of visuohaptic processing in the brain. Therefore, an overarching question concerns the integration of sensorimotor systems for object recognition across development: How do the neural mechanisms involved in multisensory visuohaptic object recognition develop? More specifically, how do these visuohaptic systems interact in the brain and change over time? Following from these questions, the primary research goal is thus to better understand the development of the neural mechanisms underlying haptic and visuohaptic object recognition.

The following work is organized in five chapters to answer the overarching question and address the research goal. The first chapter provides an introduction to the development of visuohaptic object recognition, and gives the necessary background and motivation for the three experimental studies described in the second through fourth chapters. In the fifth chapter, the findings from the current studies are summarized, a developmental trajectory is presented, and the limitations and future directions are discussed.

1.2. Visual system and motor system development

This section introduces the development of the visual and motor systems. An overview of these systems is first provided, followed by a description and evaluation of the theories and models underlying their development. The implications of these theories are discussed, particularly in light of the principle of "developmental gradualness."

1.2.1. Visual system development

In early visual development, several major subcortical and cortical pathways have been mapped out. The major subcortical pathway consists of direct projections from the retina to the superior colliculus; the retinal ganglion cell axons have been demonstrated to terminate primarily in the superficial layers of the superior colliculus (Iliescu & Dannemiller, 2008). The major cortical pathway extends from the retina to the lateral geniculate nucleus (LGN) to the primary visual cortex. This retinocortical pathway consists of two parallel processing streams that are thought to be semi-independent. These are the parvocellular and magnocellular streams which are evidenced by distinct types of ganglion cells in the retina, are separated into four parvocellular and two magnocellular layers in the LGN, and project to different layers in layer 4C of the primary visual cortex (Iliescu & Dannemiller, 2008; Livingstone & Hubel, 1988). The parvocellular, temporal-directed stream is associated with V4 and inferotemporal areas, while the magnocellular, parietal-directed stream is associated with V3, MT, MST, and posterior parietal areas (Iliescu & Dannemiller, 2008; Atkinson & Braddick, 2003). This distinction, however, which extends to the dorsal and ventral streams and will be further elucidated later on, does not imply independence in information processing. On the contrary, there is a high level of crosstalk between the two streams. In addition to the

major subcortical and cortical pathways, there are also cortical-subcortical pathways that project from the visual cortex to structures such as the superior colliculus and the LGN (Iliescu & Dannemiller, 2008).

Several theories and models have been proposed to account for the development of cortical and subcortical brain-behavior relationships. These have generally included the common notion that differential rates of maturation exist within and between subpathways in the visual system (Iliescu & Dannemiller, 2008). Although the foundations for visual circuitry are present at birth, visual processes begin and develop at varying ages and rates postnatally. It has been suggested that there are distinct functional modules comprised of linked subcortical and cortical networks, and furthermore, that subcortical functions mature earlier than cortical functions (Iliescu & Dannemiller, 2008; Atkinson & Braddick, 2003; Atkinson, 1984). As such, most of the visual behavior that can be observed in the first month of life is controlled by subcortical structures (e.g., superior colliculus), and only around two months of age do descending cortical pathways from the visual cortex to the superior colliculus mature enough for the development of other visual capabilities (Atkinson & Braddick, 2003; Atkinson, 1984).

A similar proposal by Atkinson regarding advances in maturation of the parvocellular stream over the magnocellular stream stems from observations of visual functions associated with the former stream (e.g., orientation discrimination) emerging earlier than those of the latter (e.g., direction-selectivity; Atkinson, 1992). Atkinson's two-part model describes visual development as: 1) comprised of two separate streams with differential maturation rates in which the parvocellular stream develops first; and 2) an integration across these streams for a representation of objects that serves the purpose

of object recognition and action (Atkinson, 1992). Although the second notion is widely accepted, the first is part of an ongoing debate that extends to the distinction between the dorsal and ventral pathways with regard to which stream develops first. The inconsistencies in this debate are fueled primarily by the different dependent measures that are taken, age ranges that are tested, and tasks that are used. This will be further explored in a later section (*1.3.2. Development of dorsal and ventral streams*).

1.2.2. Motor system development

Early development of motor systems involves several brain areas that function based on communication between the motor cortices, other cortical areas, and the cerebellum to name a few (Angulo-Barroso & Tiernan, 2008; James & Maouene, 2009; Diamond, 2000). The motor cortices include the primary motor cortex, which is organized somatotopically and receives input from the premotor and supplementary motor areas, as well as from the primary somatosensory cortex and cerebellum, and projects to the spinal cord for effector-specific action execution. The premotor regions receive inputs from the posterior parietal cortex, cerebellum, and supplementary motor area, and send outputs to the primary motor cortex. While the dorsal premotor region is involved in the preparation and execution of motor acts, the ventral premotor region is involved with hand movements and action observation (James & Maouene, 2009). The supplementary motor area obtains its input from the posterior parietal cortex as well, but projects to the premotor regions and the primary motor cortex for motor execution, bimanual coordination, and sequential movements. Other cortical areas include the somatotopically-organized primary somatosensory cortex, which receives thalamic input and projects to the primary motor and posterior parietal cortices for somatosensory

information perception. The posterior parietal cortex receives inputs from the primary somatosensory cortex, premotor region, and visual cortex, and outputs to the premotor regions, supplementary motor area, and cerebellum for visuomotor transformations (e.g., reaching). Lastly, the cerebellum has been implicated in numerous processes including, but not limited to, motor control and coordination, sensorimotor integration, and movement planning and learning (Diamond, 2000).

Theories have now stressed the importance of movement in early development including the action approach proposed by von Hofsten (2004), and the dynamic systems approach advanced by Thelen and Smith (1994). In the action approach to motor development, the planning of movements is crucial for understanding how skilled motor behavior emerges. These actions, from gazing to later hand orienting, are flexibly controlled as well as adaptive depending on the context (Angulo-Barroso & Tiernan, 2008; von Hofsten, 2004). In the dynamic systems approach, new forms of behavior emerge from the interaction between multiple systems; human behavior thus arises from a dynamic and adaptive interplay between complex systems with varying levels of stability. In order to accomplish a goal, a system that is both complex and adaptive creates variability, and therefore, opportunities for new modes of exploration. These can be portrayed as states and phase shifts (Thelen & Smith, 1994). Using dynamic principles, change is facilitated by the loss of stability, that is, variable movement patterns facilitate exploration for new behavioral patterns that are most adaptive for a given context. Based on these notions, four critical implications in the conceptualization of motor development in a dynamic system are as follows: 1) a child's stability in movement patterns is constantly shifting because of developmental changes in the brain,

body, and environment; 2) this stability is completely dependent on the coordination between systems; 3) changes occur due to interactions between components of each system and between systems; and 4) the child's current dynamic state is a function of previous states and sets up future states (Thelen & Smith, 1994; Angulo-Barroso & Tiernan, 2008).

Given these theories on both visual and motor system development, a critical concept is the principle of "developmental gradualness" as elucidated by Fischer and Bidell (1992). Specifically, the principle states that particular skills and abilities do not emerge fully formed in the child's behavioral repertoire (e.g., for perception, recognition, or action). Instead, these abilities appear initially in some rudimentary form in highly specific contexts, and then gradually become more complex over time and more applicable to a wider-range of contexts (Fischer & Bidell, 1992). This principle can be applied to the current theories of visual system development, which already maintain the notion of differential rates of maturation. However, these theories fail to address extrinsic factors such as context. This principle introduces the significance of varying ranges of context (and task) on development for the emergence and fine-tuning of abilities. The theories of motor development implicitly adhere to this principle, although a high level of complexity is already assumed in the dynamic systems approach.

Taken together, the implications of the theories on visual and motor development suggest that the visual and motor systems are inextricably linked; the development of both systems are constantly adapting together to a changing context, whether it be environmentally-, bodily-, or neurally-based, or more likely, as an interaction between all three.

1.3. Distinctions between the dorsal and ventral streams

Within the visual system, the earlier discussion of magnocellular versus parvocellular streams alluded to extensions in the dorsal and ventral streams. The distinction between the dorsal and ventral visual streams for action and for perception, respectively, are addressed in adults and across development.

1.3.1. Dorsal and ventral streams in adults

The existence of two separate streams, as initially formulated by Ungerleider and Mishkin (1982), specified a parceling of the types of analysis performed on the visual array (Milner & Goodale, 1995). In this distinction with its emphasis on visual input, the dorsal stream computes location attributes of a stimulus for spatial vision while the ventral stream computes other visual attributes (e.g., size, shape, orientation, and color) for object vision. Based on this parcellation, Livingstone and Hubel (1988) elaborated an account in which the distinction between dorsal and ventral streams was translated into a distinction between magnocellular and parvocellular channels. However, more current evidence suggests that these two channels are highly intermingled and are present in both dorsal and ventral stream projections. For instance, although the dorsal stream, which projects from the striate cortex to the posterior parietal cortex, receives mainly magnocellular input, the parvocellular input is still significant; in the ventral stream, both types of inputs are equally present (Milner & Goodale, 1995).

A different characterization of the distinction between the functional roles of the dorsal and ventral streams has been proposed by Milner and Goodale (1995) with an emphasis on motor output. This model of the two streams suggests that the transformations of visual input in the ventral stream that are required for perception (e.g.,

object recognition) are quite different from the sensorimotor transformations in the dorsal stream that are required for the control of action (e.g., visually guided action such as reaching). In adults, delineations have been made regarding the cortical and subcortical paths taken by each stream.

In the ventral pathway, projections from the primary visual cortex reach the inferotemporal cortex in a multitude of routes passing through areas such as V2, ventral portions of V3, and V4, where a progression in the specificity of coding visual features is observed (Milner & Goodale, 1995). Moreover, there are few, if any, descending pathways between the inferotemporal cortex and the superior colliculus, indicating a lack of visual eye movement control by the ventral stream (Milner & Goodale, 1995).

The dorsal pathway consists of projections from the primary visual cortex to the posterior parietal cortex, passing through at least three different areas (i.e., middle temporal (MT) for ocular pursuit and movement guidance, V3A for providing visual information to guide manual grasp control, and parieto-occipital (PO) for directing saccadic eye movements or manual reaching; Milner & Goodale, 1995). From there, the posterior parietal cortex links to separate areas in the prefrontal, premotor, and primary motor regions in the frontal cortex, thus forming a complex parieto-frontal visuomotor system. This pattern of neural activation has been supported by functional magnetic resonance imaging (fMRI) studies of adults performing visually guided motor tasks (Ellermann et al., 1998). Moreover, most of the dorsal stream areas send descending projections to the superior colliculus for the visual control of eye movements (Milner & Goodale, 1995). These various routes can be considered as distinct modules within the dorsal stream that allow for the control of different actions. Thus, exploratory eye

movements, as well as reaching, grasping, and manipulating objects, involve integrating the functions of different action modules (Atkinson & Braddick, 2003; Milner & Goodale, 1995).

According to the two models mentioned above, both cortical streams process information concerning object properties. However, while transformations in the ventral stream allow for the formation of perceptual representations as viewpoint-independent, transformations in the dorsal stream mediate the control of goal-directed actions by capturing the instantaneous and view-based properties needed for visuomotor control. This viewpoint dependency has been further elucidated in fMRI studies in adults examining the effects of viewpoint on dorsal and ventral stream activation. In one particular study, James and colleagues (2002) demonstrated that generalizations across viewpoints were observed in the ventral occipitotemporal cortex, an area that is part of the ventral visual processing stream. This system, which is critical for object recognition, was shown to treat the same object seen from different viewpoints as identical. Contrastingly, viewpoint dependency was observed in the caudal intraparietal sulcus, which is located in the dorsal visual processing stream and is involved in the visual control of actions. In this system, the same object presented from different perspectives required a new set of actions, and was found to be treated similarly to a novel object (James, Humphrey, Gati et al., 2002).

Although these neural mechanisms are fairly well studied and defined in adults, the developmental trajectory of the dorsal and ventral streams is unclear. While some researchers maintain that the dorsal steam develops first (Schlesinger & Limongi, 2005; Nishimura, Scherf, & Behrmann, 2009), others argue that functionality in the ventral

stream emerges earlier (Bertenthal, 1996; Atkinson, 1992; Dilks, Hoffman, & Landau, 2008). Still others take a more neutral stance in this regard, but claim that there are different rates of development between the two streams (Dilks, Hoffman, & Landau, 2008; Johnson, Mareschal, & Csibra, 2008).

1.3.2. Development of dorsal and ventral streams

In applying the dual-route visual processing model to development, several fundamental questions arise such as which of the dorsal and ventral streams functionally develops first, and whether the integration between the two pathways increases or decreases in separation with development. The answers to these questions have significant impact on the understanding of the developmental progression of sensorimotor processing, and may influence later functioning as well.

To address the first question regarding the controversy as to which stream functionally emerges first, studies have implemented computational and behavioral models. One computational study has decomposed infants' object representations into simulated dorsal and ventral stream processing, and subsequent findings support the pattern that the dorsal pathway develops first followed by a more gradual development of the ventral pathway (Schlesinger & Limongi, 2005). Contrastingly, other behavioral reports suggest that the capacity for object representation and recognition emerges at birth, while a slower developing action system emerges later (Dilks, Hoffman, & Landau, 2008; Bertenthal, 1996). Perceptually controlled actions become better tuned and coordinated with neural development and experience, however, and may follow perceptual object recognition shortly after birth.

More recent evidence has indicated that the dorsal stream may have a more

prolonged developmental trajectory relative to the ventral stream, and as such, the functions normally guided by the dorsal stream in adults appear to be underdeveloped compared to functions in the ventral stream. This developmental "delay" extends beyond infancy into childhood as demonstrated by Dilks and colleagues (2008) who tested 3- to 10-year-old children and age-matched Williams Syndrome individuals in a visually guided action task (posting a card into an oriented slot) and a visual perception task (matching a card to the slot's orientation). Based on performance measures in which children: 1) were worse at the action task (i.e., more errors were made); 2) were at ceiling in the perceptual task; and 3) demonstrated significant improvement between 4 to 6 years, these authors concluded that the dorsal stream develops more slowly and is more vulnerable to breakdown than the ventral stream (Dilks, Hoffman, & Landau, 2008).

Assuming there are distinct functional modules within the visual system (see subsection *1.3.1. Dorsal and ventral streams in adults*), different functions within the streams may emerge at different times in development; this notion can be used to account for the discrepancies in the age at which specific abilities emerge (Atkinson & Braddick, 2003; Milner & Goodale, 1995). Indeed, some dorsal stream functions have been shown to emerge later than the majority of ventral steam functions (Johnson, Mareschal, & Csibra, 2008). Based on ERP data, namely of a postsaccadic component known as the lambda wave that is evident in 6 month olds over ventral visual areas, researchers have concluded that the ventral pathway is functionally active at 6 months, with the caveat that there is room for further fine-tuning across development. The same component that is not evident over dorsal stream areas have led these researchers to believe that the control of eye movements by the dorsal pathway is not yet functionally active at this age; rather,

saccadic eye movement control may still be under subcortical influence via the superior colliculus (Johnson, Mareschal, & Csibra, 2008). However, behavioral evidence indicates that infants younger than 6 months of age are able to perform well-directed reaching to objects, which is associated with the dorsal pathway. Thus, dorsal stream directed eye movements are delayed relative to reaching, which supports differential development of multiple parallel functional modules within the dorsal pathway. This differential development likely occurs in both dorsal and ventral streams, continuing on through infancy and into childhood.

To examine the second question regarding the hypothesis that there is a dissociation between processing in the two visual pathways during development, paradigms implementing preferential looking times and habituation have been used with temporarily occluded objects. Research in 4-month-old infants during occluding events suggests that information processed separately in the dorsal and ventral streams is unable to be maintained or integrated. For instance, Mareschal and Johnson (2003) used faces and colored asterisks compared to manipulable toys in a habituation paradigm in which location, feature, or both were violated following occlusion. They discovered that a target's affordance for action determines whether the information processed by the dorsal stream (e.g., location, size, shape, but not color) or ventral stream (e.g., color, size, shape, but not location) is maintained. These authors claimed that at 4 months of age, infants demonstrate poor coordination and integration of dorsal and ventral object representations, although both streams are functional. It is not until the first year that these streams begin to integrate. Furthermore, a secondary claim argues that the maintenance of information processing or elicitation of one stream over another is

strongly dependent on the stimuli used in a paradigm (Mareschal & Johnson, 2003).

To summarize, although there are disagreements among researchers as to which stream develops first, a general consensus is that both streams do become more integrated with development. Given these findings, there are several issues that come to mind. One issue concerns the assumption of developmental linearity such that one stream or another *must* develop first. Notwithstanding, many studies have now indicated U-shaped performance curves as a function of age, and thus nonlinear developmental trajectories. It remains unknown whether the presumed head start of the ventral stream maintains a constant lead over the dorsal stream until both pathways stabilize, or whether there is a period of time during which the dorsal stream leaps forward. Moreover, as noted by Mareschal and Johnson (2003), depending on the task, stimuli, and dependent measures used, highly disparate conclusions may be drawn. This last point concerns the generalizability between research findings. For instance, results obtained from measuring competencies in one system (e.g., eye movements) may not be demonstrated by other systems (e.g., reaching) at the same age. Therefore, development with regard to a specific behavioral dependent measure may not translate to the emergence of a specific ability or the development of underlying neural mechanisms. Nevertheless, it has been established that the dorsal stream is responsible for visually guided action, while the ventral stream is responsible for visual object perception and recognition in both children and adults.

1.3.3. Perception and action across development

Given that there is an inherent link between vision for perception and vision for action, perhaps these two functionally distinct systems cannot be so easily dissociated. It is not clear where a line can be drawn between vision for perception versus for action, as both

systems are essential for perceiving the world and acting in it. Moreover, neuroimaging data has implicated bidirectional influences in which sensorimotor experience augments activity in the ventral stream, and purely perceptual inputs similarly activate dorsal visuomotor regions.

In one direction, neuroimaging studies conducted on children have indicated that sensorimotor experience enhances processing in the visual system. One particular study testing 4- to 5-year-old children examined the percent signal change of the blood oxygen level dependent (BOLD) response, which increased significantly in a putative visual area (i.e., the fusiform gyrus) after active sensorimotor learning of letters compared to passive, visual learning (James, 2009). Thus, visual areas may integrate inputs from other sensory modalities, as well as from the motor system; perceptual processes are not strictly encapsulated modules, but rather can, and do, receive feedback from sensorimotor processes (James, 2009). This suggests a very strong coupling between perceptual and action (motor) systems.

In the other direction, purely perceptual (e.g., visual) presentations of stimuli with which children have had prior active experiences result in activations of cortical motor areas responsible for those actions (Smith, 2009). For instance, after actively exploring novel objects, 5 to 6 year olds showed motor cortex activity during visual (and auditory) perception; this activity was more enhanced than passively perceiving an experimenter interact with the objects (James & Swain, 2011). These results indicate that sensorimotor systems develop with increasing interactions and active experiences, lending support to the theory of common coding that action and perception share a common representational domain (Prinz, 1997). The shared representations can be accessed solely via perception as

they contain the relevant motor plans that have been coupled to that perception through experience.

Further to the point, just as action may elicit increased activity in visual cortices, and just as perception can activate motor cortices as well, perception can even recruit visuomotor regions without concurrent movement (James & Gauthier, 2006). In a task comparing 6- to 10-year-old children to adults, passive viewing of tools activated regions in the ventral stream (e.g., LOC), as well as in the dorsal "grasping-circuit" (e.g., intraparietal regions including AIP, LIP, VIP, and the inferior frontal gyrus; Dekker, Johnson, Mareschal, & Sereno, 2010). This purely perceptual task involving no action whatsoever was not only able to recruit visual processing areas, but also able to recruit dorsal visuomotor regions. Moreover, both children and adults showed similar patterns of activity in response to the visual stimulus, indicating that these cortical regions may be organized in an adult-like manner by 6 years of age (Dekker, Mareschal, Sereno, & Johnson, 2011; Dekker et al., 2010).

In light of these findings, perception and action in vision, or in any other modality for that matter, must be considered dynamically, where sensory and motor processes mutually interact with, influence, and constrain one another. As such, the development of the predominant visuomotor system in the dorsal stream is intrinsically linked to the development of the perceptual system in the ventral stream. Although there may be distinct functional modules with differential rates of development based on experience and maturation in each stream, they combinatorially comprise the sensorimotor system. Moreover, analogous to the visual system in which the functional processing between the dorsal and ventral pathways can be differentiated as vision for action and vision for

perception, a similar distinction can be made in the haptic modality. Each of these unisensory systems are discussed in the following section in terms of object recognition.

1.4. Unisensory systems in object recognition

Two of the most important unisensory systems supporting object recognition include vision and haptics. Although a multitude of behavioral studies have been conducted on these systems, this section primarily focuses on the neural bases of the visual and haptic systems in adults and children (with the exception of haptic object recognition in children for which only behavioral studies have been conducted).

1.4.1. Visual object recognition

In adult visual object recognition, the notion of two parallel streams, the dorsal stream and the ventral stream, between higher-order processing regions in the parietal lobe and early visual areas in the occipital cortex is widely held (see subsection **1.3. Distinctions between the dorsal and ventral streams**; Ungerleider & Mishkin, 1982; Ungerleider & Haxby, 1994). A functional distinction based on the motor output is made between the dorsal and ventral streams as, respectively, vision for action and vision for perception (Goodale et al., 1994; Milner & Goodale, 1995). According to this model, the sensorimotor transformations of visual input needed for the control of actions in the dorsal stream (e.g., for visually guided action) are implemented quite differently from the same visual input that is transformed for perception in the ventral stream (e.g., for object recognition).

The dorsal visual pathway, projecting from visual cortex to posterior parietal cortex, is designated for actions upon objects such as visually guided reaching. This

forms the predominant basis of visuomotor processing in the visual system. Within the ventral visual pathway for object representation and recognition, a vigorous investigation surrounds the organization and function of the lateral occipital complex (LOC), which is located within the lateral occipital cortex (Malach et al., 1995; Grill-Spector, Kourtzi, & Kanwisher, 2001; Kourtzi & Kanwisher, 2001). This structure has been shown to respond to intact (images of, and three-dimensional forms of) objects as compared to scrambled versions of the same objects or textures (e.g., Amedi et al., 2001, 2002, 2005; James et al., 2005; James & Kim, 2010). Moreover, evidence has been provided that the LOC represents shape rather than contours or low-level visual cues (e.g., color or texture) that help to define an object (Grill-Spector, Kourtzi, & Kanwisher, 2001).

Developmentally, visual object perception emerges in infancy and continues to develop rapidly until an arguably adult-like level is reached in early childhood for recognizing basic objects. Behavioral studies have even demonstrated that young infants are able to recognize simple, three-dimensional shapes, and may have some understanding of shape parts (Nishimura, Scherf, & Behrmann, 2009). However, the ability to recognize more complex objects develops slowly and through adolescence. For example, visual proficiency in certain tasks examining grating acuity and orientation discrimination does not become adult-like until sometime between 6 to 7 years (Grill-Spector, Golorai, & Gabrieli, 2008). In fMRI research comparing children and adolescents to adults during visual object perception tasks, visual presentations of stimuli have been shown to activate the LOC located in the ventral stream. Two particular studies have indicated that children as young as 5 to 8 years of age demonstrate adult-like category selectivity for objects in this region (Grill-Spector, Golorai, & Gabrieli, 2008;

Scherf et al., 2007). In one study, consistent bilateral activity in the LOC was found in response to objects in children (5 to 8 years), adolescents (11 to 14 years), and adults (Scherf et al., 2007). Results indicated no differences between or within groups in terms of the site, extent, and magnitude of BOLD activation for objects in the LOC, indicating adult-like processing by 5 years. However, differential developmental patterns have been found in this region for faces, places, animals, and objects from unusual views, which show a more protracted developmental trajectory extending beyond 7 years to reach an adult-like level of processing (Grill-Spector, Golorai, & Gabrieli, 2008; Scherf et al., 2007; Dekker et al., 2011). This suggests that additional experience is required for the recognition of these more complex classes of stimuli. Thus, differential rates of development for processing various types of stimuli exist in the ventral visual stream, analogous to the differential rates of maturation of distinct action modules in the dorsal stream.

Similar to visual object recognition, several developmental trajectories have also been proposed for object recognition within the haptic modality. Moreover, just as there is a distinction in the visual system regarding the dorsal and ventral pathways as vision for action and perception, respectively, the haptic system can also be separated into distinguishable and parallel streams that process information differentially.

1.4.2. Haptic object recognition

It has been well established that the adult haptic system is highly efficient at extracting the properties of an object, and exploiting that information for recognition (Klatzky, Lederman, & Reed, 1987; Lederman & Klatzky, 1990; Lederman & Klatzky, 1993). Haptic object processing has been defined as the "active use of the hands to retrieve the

attributes of an object stimulus, using both cutaneous and kinesthetic inputs" (James, Kim, & Fisher, 2007). These sensory inputs are processed via (at least) two distinct neural pathways, one for geometric properties such as shape, and another for material properties including texture. Moreover, the haptic pathway for shape processing has been divided into two different streams for action and for perception, analogous to vision. These have also been called the dorsal and ventral streams, or the "where" and "what" streams, respectively (Ungerleider & Mishkin, 1982; Milner & Goodale, 1995). While the dorsal stream is responsible for coordinating actions and motoric behaviors directed toward objects, the ventral stream is responsible for the recognition of objects (Johnson, Mareschal, & Csibra, 2008).

Within the somatosensory system, haptic object localization is processed in the superior parietal areas while object identification is processed in the inferior parietal areas (Lederman & Klatzky, 2009; Reed, Klatzky, & Halgren, 2005). In the haptic system more generally, the anterior region of the intraparietal sulcus (aIPS) along the dorsal side of the brain processes geometric object properties (i.e., shape) for object-directed motor actions (James & Kim, 2010). This region has been shown to demonstrate a preference for overall shape as compared to shape primitives (e.g., curvature, T-junctions, etc.; Bodegard et al., 2001), and is where activation has been found in response to haptic stimuli comprised of everyday, familiar objects (Amedi et al., 2001, 2002; Deibert et al., 1999; Reed, Shoham, & Halgren, 2004; see Amedi et al. (2005) for a review), as well as simple, geometrical shapes (Bodegard et al., 2001; Roland et al., 1998). Furthermore, this region has been associated with the integration of somatosensory and motor information (James, Kim, & Fisher, 2007). On the ventral side of the brain within the lateral occipital

complex (LOC), the lateral occipital tactile-visual region (LOtv) is primarily involved with processing shape information about objects for haptic recognition (Amedi et al., 2001, 2002; James & Kim, 2010; James et al., 2005).

In addition to the aIPS and LOtv, a plethora of neuroimaging studies has implicated several other brain regions that are associated with haptic object exploration and recognition (James, Kim, & Fisher, 2007; Reed, Shoham, & Halgren, 2004; Bodegard et al., 2001; Binkofski et al., 1999). The postcentral gyrus, which houses the primary somatosensory cortex (SI), sends information down to the parietal operculum, or the secondary somatosensory cortex (SII). Due to the connections between the SII and motor cortex, this region has been demonstrated to play a role in active exploration, and as such, may provide sensory feedback for the manipulatory movements necessary for obtaining salient object information. The SII has also been shown to be involved in processing the material properties of objects, and though important for haptic object recognition, this area is presumed not to be involved in shape processing (James, Kim, & Fisher, 2007). Based on these findings, adult haptic object recognition seems to involve a complex interaction between motor and somatosensory systems, as well as between the macrogeometry (e.g., overall shape) and microgeometry (e.g., texture) of perceived objects (James, Kim, & Fisher, 2007).

Across development, there is a blatant lack of research regarding the neural correlates of haptic object recognition in children, which is a gap that the current work seeks to fill. The studies that have been conducted have been primarily behavioral due to the difficulties in neuroimaging children during haptic tasks, which necessarily involve a lot of motion. In developmental populations, behavioral studies investigating haptic

object recognition have tested children for their ability to identify, recognize, and manipulate different objects. Several studies regarding the identification of objects have implemented paradigms requiring children to label objects. These results demonstrated that children as young as 2.5 years are able to identify and recognize a high proportion of common objects by touch alone (Bigelow, 1981); other studies have shown that children from 3 years and on are also able to correctly identify familiar objects (Morrongiello et al., 1994). Studies examining the development of haptic recognition and object manipulation have implemented behavioral match-to-sample paradigms. Bushnell and Baxt (1999) showed that 5-year-old children demonstrate excellent unimodal haptic to haptic recognition for both familiar and novel objects. Furthermore, according to research conducted by Kalagher and Jones (2011), children from 3 to 5 years of age begin to acquire more mature, adult-like behaviors in terms of their exploratory procedures during haptic manipulation of objects.

Yet, there is a high degree of inconsistency within the literature regarding the age at which infants and children are able to perform haptic exploratory procedures. While Bushnell and Boudreau (1993, 1998) suggested a developmental trajectory that encompasses all types of exploratory procedures between the ages of 3 months to 1 year, other studies have reported that these abilities emerge anywhere between birth and 5 years (e.g., Streri & Feron, 2005; Kalagher & Jones, 2011). In this debate, although some researchers do take a more conservative stance and note the rudimentary form of infant haptic exploratory behaviors, namely Bushnell and Boudreau (1993, 1998), the majority of researchers seem to have concluded that the sensory and motor systems are present and fully formed at birth, or shortly thereafter (Streri & Feron, 2005). These studies have

reported precocious exploratory abilities in even newborns (Streri, 1993; Streri & Feron, 2005; Streri, Lhote, & Dutilleul, 2000; Steri & Molina, 1993).

Given the discrepancies between reported ages of ability with regard to Lederman and Klatzky's exploratory procedures (1987), the principle of "developmental gradualness" may be applied to haptic abilities. Although infants may demonstrate precursory abilities that eventually result in mature, adult-like exploratory procedures, their initial forms of haptic exploration are subject to this principle in that they are not yet fully formed. In children, this principle once again applies, albeit at a higher level of scaling. As younger children are exposed to more objects and gain experience interacting with those objects in a wider range of contexts, their behavioral repertoire becomes more complex to reflect this increased experience. Nevertheless, by 5 years of age, children seem to have developed fairly adult-like behavioral movements for recognizing objects haptically (Kalagher & Jones, 2011). This does not preclude further neural development, however. Similar to visual object recognition in the LOC in which basic shape processing is adult-like in young children, but the processing of more complex stimuli continues to develop, neural activity for haptic object recognition may also continue to change with experience. The neural development of haptic processing is simply unknown. Thus, the current work seeks to examine the neural correlates underlying haptics, as well as the development of visuohaptic object processing.

1.5. Multisensory object recognition

Regarding both visual and haptic systems, it has been proposed that the motor system enhances the sensory system (i.e., action for perception; Lederman & Klatzky, 1987) and

vice versa, that the sensory system enhances the motor system (i.e., perception for action). More generally, the functional dissociation between streams for object processing (i.e., "what" stream) and for spatial processing (i.e., "where" stream) that is present in both visual and haptic modalities suggests that this organizational principle within the brain is not modality-specific (Reed, Klatzky, & Halgren, 2005; Westwood & Goodale, 2003). Extending beyond unisensory object recognition, there has been a recent surge of research concerning multisensory object recognition (Calvert, Spence, & Stein, 2004). In adults, these have involved visuohaptic convergence of information from visual and haptic sensory channels (Amedi et al., 2001, 2002; James et al., 2002; James & Kim, 2010). Prior to discussing the multisensory systems that subserve visuohaptic processing and object recognition, some terminology associated with the concept of "multisensory" is first addressed below.

1.5.1. Definitions of "multisensory"

Multisensory can refer to stimulus properties or neural processes. In terms of stimulus properties, multisensory ones are not confined to a single sensory modality; rather, the properties describe multiple sensory modalities and may not be modality-specific. For instance, a multisensory object such as an apple has properties that are available to several sensory systems such as vision, haptics, and gustation. In contrast, a modality-specific property of an apple (e.g., red) may be captured visually by a two-dimensional image of that apple. *Multisensory* can also describe any form of neural process that is associated with multiple sensory modalities (Stein et al., 2010). As a general overarching term that is used to describe processes involving at least two sensory modalities, but that does not specify the exact nature of the interactions between those modalities,

multisensory processing has been used broadly in perceptual and neural domains including crossmodal matching and multisensory integration or convergence (Stein et al., 2010).

Crossmodal can refer to stimulus properties, cortical regions, or processes. In describing an object, "crossmodal" includes a complex of (usually) two modality-specific stimuli from different sensory modalities (e.g., vision and haptics; Stein et al., 2010). Crossmodal areas are defined as those that are activated only when information from at least two different sensory modalities is compared (Hadjikhani & Roland, 1998). Crossmodal matching is the process by which stimuli from different sensory modalities are compared in order to estimate their equivalence, namely, by testing whether an association between stimuli has been established (Stein et al., 2010). This involves identifying the shared information between two objects while preserving the stimulation characteristics from each modality's input. Crossmodal processing has been demonstrated to occur not only in multisensory regions, but also in putative unisensory regions located very early on in the cortical processing stream (Merabet & Pascual-Leone, 2008).

Multisensory integration refers to a general process in which at least two different unisensory signals interact and combine to form a new product, or neural signal, that is significantly different from the component inputs. This form of integration has been defined as a response that differs from (i.e., is smaller or larger than) the summed responses evoked by the individual modality-specific stimuli (Stein et al., 2010). Similarly, *multisensory convergence* describes a process in which the responses to inputs from multiple sensory modalities overlap. This results from stimulus-driven activation of neurons in specific cortical areas by the inputs of at least two different sensory channels.

Based on multisensory neurophysiology and single-unit recordings, two types of multisensory convergence can be distinguished: areal and neuronal convergence (Meredith, 2002). Areal convergence describes the projection of different sensory inputs onto the same neural region, but not onto the same neurons. As the sensory inputs do not synapse on the same neurons, they do not become integrated. Neuronal convergence describes the synapsing of different sensory inputs onto the same neurons, which results in an integration of the sensory signals. Thus, the convergence of visuohaptic signals may reflect either sensory processing by a population of interspersed unisensory neurons, or multisensory integration in neurons that process both visual and haptic inputs (James & Kim, 2010; Kim & James, 2010; Lacey & Sathian, 2014). As single-unit recording is extremely difficult to perform in humans, functional neuroimaging may be used as a non-invasive alternative to capture multisensory convergence (with the caveat that this method measures populations of neurons and additional criteria must be used to determine neuronal convergence). In multisensory research, *convergence* and *integration* are often used interchangeably; in the chapters to follow, *multisensory convergence* is the primary term used to describe the experimental studies.

1.5.2. Multisensory object processing in adults

Multisensory systems, specifically visuohaptic systems, are highly involved during object recognition in adults, and are supported by evidence from neural measurement techniques such as fMRI, and from behavioral measures.

Neural evidence. Many studies have now demonstrated two sites of multisensory convergence in the ventral and dorsal streams of the visual and haptic systems. According to one model, while multisensory shape cues for object perception are processed at the

convergence of the ventral pathways of the visual and haptic systems, convergence of the dorsal pathways in both modalities permits the processing of object shape for object-directed motor actions (James & Kim, 2010). This is evidenced by several fMRI studies that have demonstrated neural overlaps between regions that process visual and haptic shape for object recognition, as well as for sensorimotor interactions with those objects (James & Kim, 2010; Amedi et al., 2001; James et al., 2002; Grefkes et al., 2002). The overlapping cortical substrates include the ventrally-located lateral occipital complex (LOC) and the dorsally-located intraparietal sulcus (IPS).

Located in the ventral stream, it has been shown that the LOC responds not only to visual presentations of objects, but also to haptic presentations of those objects as well (Amedi et al., 2001, 2002; James et al., 2002; Stilla & Sathian, 2008). One particular cortical region that has commonly been recruited is the lateral occipital tactile-visual region (LOtv). However, it is arguable whether this region demonstrates complete modality-invariance (Grill-Spector, Kourtzi, & Kanwisher, 2001; James & Kim, 2010; Dijkerman & de Haan, 2007), or is instead bisensory in nature and responds only to visual and haptic inputs (James et al., 2005). The latter argument is supported by neuroimaging evidence suggesting that auditory cues do not activate this area or the greater LOC (Amedi et al., 2002; James et al., 2005). With this debate aside, however, it is generally agreed upon that LOtv demonstrates a generic preference for, and is recruited by, the processing of object shape.

During interactions with objects, haptic exploration produces neural activation in the somatosensory cortex, as well as in areas of the occipital and parietal cortices that are associated with visual processing (James et al., 2002; Amedi et al., 2005). One particular

region located in the dorsal stream, the IPS, has been implicated not only in haptic object processing, but also in the processing of visuomotor object-directed actions such as the control of eye movements and of visually guided pointing, reaching, and grasping movements (James, Kim, & Fisher, 2007). Furthermore, the IPS has been shown to be a site of convergence for a multitude of sensorimotor processes that depend heavily on visual, haptic, and motor information for the analysis of object shape (James & Kim, 2010).

Thus, based on the neural evidence, the LOtv and the IPS are two convergence sites of separate dorsal and ventral pathways within the visual and haptic systems. The LOtv involves visual and haptic processing of shape information for object recognition, while the IPS processes this information via sensorimotor transformations for guiding object-directed actions. As such, both the LOtv and the IPS seem to be recruited based on the shape characteristics of objects whether it be for object recognition or for object exploration and interaction (Grefkes et al., 2002; Peltier et al., 2007; Bodegard et al., 2001; James et al., 2002; Stilla & Sathian, 2008; James & Kim, 2010). Therefore, there are overlapping regions in which visual and haptic inputs converge along both dorsal and ventral streams in the adult brain, forming the integrated and multisensory visuohaptic system for object recognition.

Behavioral evidence. In order for correct sensorimotor transformations to occur during multisensory object recognition, the ventral and dorsal streams of the visual, haptic, and motor systems must be integrated. These systems are not isolated during object processing in typically functioning adults. Rather, there is a sensorimotor continuum in which these systems are highly integrated, making it difficult to separate

object processing into its constituent visual, haptic, and motor components (Tucker & Ellis, 2001).

Behavioral evidence in support of the integrative processing of visuohaptic inputs for object recognition has been demonstrated in studies implementing crossmodal paradigms. For instance, crossmodal priming studies have shown an efficient sharing of object information across the visual and haptic sensory modalities (Rentschler et al., 2004; Ernst, Lange & Newell, 2007). "Priming" in this case refers to a facilitatory effect of prior exposure to a stimulus on subsequent perceptions of that stimulus, during which the subject is often unaware of the effect (James et al., 2002). Using the findings from these studies as a foundation, Ernst and colleagues (2007) implemented an old-new recognition paradigm while recording recognition performance for objects in unimodal and crossmodal conditions. Results indicated that although different aspects of the object's shape were encoded by the visual and haptic systems, these systems provided complementary information about the same object shape. More importantly, however, their results showed that once the encoded information was matched across modalities, no cost in recognition performance (i.e., percentage correct) was observed for crossmodal versus unimodal conditions. These findings provide evidence that shape information obtained from these different sensory modalities can easily be shared (Ernst, Lange, & Newell, 2007).

Three possible candidate models have been proposed to explain this sharing or combining of information across the sensory modalities. The first model advocates the notion that information about objects is independently maintained in modality-specific formats, but is accessible by amodal systems (Ernst, Lange, & Newell, 2007). This,

however, has been refuted in studies conducted on the congenitally blind in which vision has been restored. For instance, Held and colleagues (2011) demonstrated that newly sighted patients performing a behavioral match-to-sample task of object shape based on haptic to visual inputs were unable to transfer their haptic knowledge of shape to the visual domain (Held et al., 2011). Thus, this inability to reconcile object shape information from the two different sensory modalities without prior experience provides evidence against an amodal system.

The second model proposes that information can be recoded directly from one sensory modality to another (Ernst, Lange, & Newell, 2007). According to this model, objects felt via touch can be transformed directly to the visual modality. However, while studies have shown that information can be shared efficiently across sensory modalities, there is not enough substantial evidence to claim a *direct* recoding process between the two modalities. Matching representations of objects (within a scene) across vision and haptics may even be suboptimal, resulting in a cost in recognition performance (Newell et al., 2005). This notion stems from differences in encoding procedures between vision and haptics; while vision can process stimuli in a parallel manner, haptics requires a sequential integration of stimuli over time (Newell et al., 2005). Thus, the differences in encoding may be enough to refute a theory suggesting a direct recoding of information. Others, however, have argued that vision and haptics share very similar object representations in terms of shape such that they may even share the same neural substrate (James et al., 2002; Amedi et al., 2005). This ties into the next possible model to explain information sharing across the modalities.

The third model suggests that information is represented in an amodal or

multisensory form (Ernst, Lange, & Newell, 2007). Although it may be a stretch to claim that *all* information is represented either amodally or multisensorily, it is possible that shape information can be represented in such a fashion that it may be accessed very quickly visually and/or haptically. This is substantiated by overlapping activity in cortical areas such as the LOtv during visual and haptic processing of object structure (James et al., 2002).

Overall, the processing of visuohaptic inputs for object recognition appears to be highly integrative. An abundance of neural and behavioral evidence suggests that there is a systemic integration of visual, haptic, and motor processes for object recognition in the dorsal and ventral action and perception streams. This tight coupling between the systems allows multisensory object processing to occur quickly and efficiently. Although the exact theories and models by which this integration occurs are debated, there is generally a consensus with regard to the neural substrates underlying multisensory object recognition in adults. Developmentally, however, very little is known about the neural correlates of visuohaptic object processing.

1.5.3. Multisensory object processing across development

Neural evidence. Activity in the visual and haptic systems is clearly interlocked across development; activity in the visual system is mapped to the haptic system, and vice versa, activity in the haptic system is mapped to the visual system (Smith, 2005). These mappings allow the processing of qualitatively different forms of information to be correlated in time. Yet, it still remains unknown how the developing brain changes over time to support multisensory object processing, although findings from adult studies may provide a guide to its development. Thus, the research studies described in the ensuing

three chapters attempt to address this gap in knowledge programmatically while using adults as a comparison.

Behavioral evidence. Relatively more research has been conducted using behavioral paradigms when working with development populations. Studies have shown that the development of object recognition becomes increasingly multisensory with concurrent streams of input from the visual and haptic modalities. From 3 to 5 years of age, children begin to acquire adult-like behaviors when manipulating haptic objects (Kalagher & Jones, 2011), and by 5 years, children perform visual, haptic, and crossmodal recognition tasks quite successfully (Bushnell & Baxt, 1999). By 6 years, object recognition has appeared to reach a state of stability as children seem to be performing at an adult-like level in many respects (Kalagher & Jones, 2011; Klatzky, Lederman, & Mankinen, 2005). Behaviorally, these include the abilities to coordinate sensorimotor inputs and recognize objects visually, haptically, visuohaptically, and crossmodally, to perform exploratory procedures for gaining information about object properties, and to relate objects to other objects functionally and multimodally (e.g., tool use), among many other skills (Kalagher & Jones, 2011; Klatzky, Lederman, & Mankinen, 2005).

While behavioral evidence shows multisensory object recognition to be highly developed by 5 to 6 years, the paucity of neural evidence in children is problematic. As such, there are limitations of the current research in child development concerning when subcomponents of the visual and haptic systems in the brain reach full stabilization prior to adulthood, if at all. This notion is based on the dynamic systems approach in which the

state of a system is constantly shifting due to developmental changes in the brain, body, and environment (see subsection *1.2.2. Motor system development*).

1.5.4. Developmental theories for multisensory perception

Visuohaptic systems are not likely to follow a linear trajectory of development for object recognition. Yet, as mentioned earlier in this chapter, traditional theories of visual and motor development do rely on sequential processes that pave the way for later developmental changes in perception and action. This type of theory assumes a very linear developmental progression where abilities build on top of maturational processes and on one another. By contrast, more recent theories such as the dynamic systems approach have now argued for a process-based account in which new behaviors emerge from complex interactions between multiple systems with varying levels of stability (Thelen & Smith, 1994). Through the loss of stability, a system that is both complex and adaptive facilitates change in the form of new behavioral patterns, and by extension neural patterns, that are optimal for a given context. The loss of stability required for change, however, implies that throughout the entire course of development, a child's, or even adult's, stability in perceptual and action abilities is continuously shifting due to changes in the brain, body, and environmental context. Moreover, stability in one system depends on coordinated activity between systems. Thus, change occurs continuously and via interactions between multiple systems, as well as between the components of each system.

Fairly recently, two distinct theoretical views have argued for multisensory development as progressive: 1) basic perceptual multisensory abilities are not present at birth, but emerge gradually over the course of a couple of years based on active

exploration and experiences of the world; and 2) these abilities are present at birth and are increasingly differentiated and refined through experience (Lewkowics & Ghazanfar, 2009; Wallace, 2004). Yet, studies have indicated a third alternative, that is, multisensory development is a regressive process of perceptual narrowing (for a review, see Lewkowics & Ghazanfar, 2009). This view proposes that perceptual tuning at birth is initially very broad, and is based on findings of neonatal abilities to perform multisensory matching. With increased experience, however, perceptual capacities become tuned, or narrowed, depending on the environmental context in which the infant is developing. In short, changes in multisensory processing based on previous experience influence the way in which objects may be perceived later in development.

As yet, there is not enough substantial evidence to indicate whether multisensory perception develops progressively or regressively (although it might be safe to assume that, regardless, experiential components are crucial for its normative development). Multisensory processing abilities are both scaffolded and constrained by the development of the sensory visual and haptic systems, as well as the motor system. Moreover, perception and action cannot be dissociated as separate developmental agents (Soska, Adolph, & Johnson, 2010). Instead, emerging perceptual abilities guide active exploration, which in turn are influenced by the development of new motor skills. For instance, when children explore objects visually, haptically, or visuohaptically, their perceptual and motor abilities constrain their exploratory actions. Simultaneously, the ways in which children actively explore and manipulate objects can influence their perceptions. Finally, to close the loop, children's perceptual abilities and exploratory behaviors also combine to create opportunities for acquiring new motor skills.

Using this sort of framework, multisensory object processing can be conceptualized as comprising many interconnected systems. Each component within the visual, haptic, and motor systems develops according to differential rates of maturation, and is dependent on experience and contextual factors. Thus, the development of visuohaptic convergence may follow a protracted trajectory compared to the individual systems, as it entails more complex forms of object processing. Multisensory object recognition likely involves highly complex interactions within, as well as bidirectional connections between, multiple neural regions.

1.5.5. Measures of functional connectivity

Measures of functional connectivity can be used to elucidate the development of connections between regions in the brain. Generally, functional connectivity refers to the temporal correlation or synchronization in activation between the time courses of two brain regions (Friston, 1994; Büchel and Friston, 2001; Koshino et al., 2005). The primary assumption underlying this type of analysis is that more synchronized regions across time will indicate higher correlation coefficients than regions that are less synchronized. This analysis consists of a multistep process including the selection of seed regions-of-interest (ROIs), the calculation of correlations between the time courses of those regions, and the creation of a matrix of resulting correlation coefficients to be tested for significance or used for more complex network measures (Varoquaux & Craddock, 2013; Koshino et al., 2005; Sporns, 2011). Functional connectivity can be captured from resting-state fMRI, or from task-based fMRI. In the present work, the general form of psychophysiological interaction (gPPI) methods of analysis is implemented to measure the changes in task-dependent functional connectivity between multisensory neural

systems across several developmental age groups (Friston et al., 1997; McLaren et al., 2012).

General psychophysiological interaction analyses aim to identify task-related changes in functional connectivity between two brain areas (O'Reilly et al., 2012). This method includes three types of regressors: (1) the variables of the experimental paradigm (i.e., psychological predictors); (2) the measurements of neural activity in a specific cortical region or seed ROI (i.e., physiological predictors); and (3) the interaction between the first two predictors (i.e., psychophysiological interactions). In gPPI, the neural responses of one cortical region are explained in terms of the interaction between the seed ROI and a task-related, cognitive (or sensory) process (Friston et al., 1997; Neufang et al., 2008; McLaren et al., 2012). In short, the functional connectivity or synchrony between two regions is measured by contrasting different psychological conditions, extracting the neural response from the seed ROI, and correlating the time course of that seed ROI to other cortical areas (McLaren et al., 2012; O'Reilly et al., 2012).

Similar measures of functional connectivity have been used to investigate the integration of networks involved in multisensory object recognition in adults. Previous research examining functional connectivity during object shape perception has implicated a bidirectional and covarying interaction between the putatively visual part of LOC and the multisensory aspect of the IPS, as well as other motor and somatosensory regions in both hemispheres (Deshpande et al., 2008). While this study only investigated task-related functional connectivity in adults, it nevertheless provides further support for known multisensory convergence areas as highly interconnected regions that are

statistically well-correlated in terms of time-dependent activity during perceptual object recognition tasks.

Across development, the ability to recognize objects in the environment both visually and haptically emerges early on, yet the development of the neural mechanisms for integrating visual and haptic object shape information remains unknown. Moreover, differences in functional connectivity across development with respect to visual and haptic object recognition are also unknown. In children, gPPI can be implemented on BOLD fMRI data to study the changing dynamics of functional connectivity through development, and to tease apart the relative contributions of specific ROIs or cognitive tasks to the neural responses of other brain regions. Generally, these analyses can be used to address questions regarding not only how strong the connections are between different brain regions depending on the task, but also how these connections change over the course of development.

1.6. Current studies

There is currently a paucity of research surrounding the neural development of multisensory object recognition. Although visual development has been well studied in the brain, this is not so for haptic or visuohaptic development. Thus, the following three chapters describe in detail three studies implementing functional magnetic resonance imaging (fMRI) and general psychophysiological interaction (gPPI) measures to better understand the development of visuohaptic object recognition. Using fMRI, the second chapter investigates the neural mechanisms underlying the convergence of visual and haptic object preference across several developmental age groups, and lays the

foundation for the subsequent studies. The third chapter examines the neural mechanisms supporting crossmodal processing during sequential visuohaptic object recognition. The fourth chapter implements gPPI methods of analysis to measure the developmental changes in functional connectivity between pre-established areas of multisensory visuohaptic convergence and other neural regions. Combined, these studies fill the gaps in our present knowledge and create a more cohesive foundation for future developmental studies examining the neural mechanisms of multisensory visuohaptic object processing.

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Chapter 2.

Multisensory Convergence of Visual and Haptic Object Preference Across Development

Abstract

Visuohaptic inputs offer redundant and complementary information regarding an object's geometrical structure. The integration of these inputs facilitates object recognition in adults. While the ability to recognize objects in the environment both visually and haptically develops early on, the development of the neural mechanisms for integrating visual and haptic object shape information remains unknown. In the present study, we used functional Magnetic Resonance Imaging (fMRI) in three groups of participants, 4 to 5.5 year olds, 7 to 8.5 year olds, and adults. Participants were tested in a block design involving visual exploration of two-dimensional images of common objects and real textures, and haptic exploration of their three-dimensional counterparts. As in previous studies, object preference was defined as a greater BOLD response for objects than textures. The analyses specifically target two sites of known visuohaptic convergence in adults: the lateral occipital tactile-visual region (LOtv) and intraparietal sulcus (IPS). Results indicated that the LOtv is involved in visuohaptic object recognition early on. More importantly, object preference in the LOtv became increasingly visually dominant with development. Despite previous reports that the lateral occipital complex (LOC) is adult-like by 8 years, these findings indicate that at least part of the LOC is not. Whole-brain maps showed overlap between adults and both groups of children in the LOC. However, the overlap did not build incrementally from the younger to the older group,

suggesting that visuohaptic object preference does not develop in an additive manner. Taken together, the results show that the development of neural substrates for visuohaptic recognition is protracted compared to substrates that are primarily visual or haptic.

2.1. Introduction

Object recognition is ubiquitous and essential for interacting with the surrounding environment. Information from various sensory channels converges to guide perception and action. Percepts are driven by the interaction of multisensory inputs and past experiences, which are the direct result of our choice of actions. Vision and haptics are two modalities in particular that offer redundant and complementary information about the geometrical properties of objects (Amedi et al., 2005). The most synergistic interactions between the visual and haptic systems occur predominantly during shape and texture processing (James et al., 2005).

Within the adult ventral visual stream, a vigorous investigation surrounds the organization and function of the lateral occipital complex (LOC), which is located within the lateral occipitotemporal cortex and encompasses the middle occipital areas and fusiform gyrus (Grill-Spector, Golarai, & Gabrieli, 2008; Grill-Spector, Kourtzi, & Kanwisher, 2001; James et al., 2002a, 2002b; Kourtzi & Kanwisher, 2001; Malach et al., 1995; Tootell et al., 1996). The LOC is intimately involved in visual object recognition. It responds strongly to three-dimensional objects and two-dimensional images of objects, and responds only weakly to scrambled versions of 2-D object images or to textures (Amedi et al., 2001; Malach et al., 1995). Additionally, the LOC responds not only to visual presentations of objects, but also to haptic presentations of those objects (Amedi et

al., 2001, 2002; James et al., 2002b; Stilla & Sathian, 2008).

Haptically, adults are highly efficient at extracting properties of objects, and exploiting that information for recognition (Klatzky, Lederman, & Reed, 1987; Lederman & Klatzky, 1993; Lederman & Klatzky, 1990). During haptic object recognition, the exploration of three-dimensional objects produces neural activation in the primary and secondary somatosensory cortices, as well as areas of the occipital and parietal cortices that are associated with visual object recognition (Amedi et al., 2005; James et al., 2002a, 2002b; Reed, Shoham, & Halgren, 2004; Sathian et al., 1997; Stilla & Sathian, 2008). In addition to the LOC, the intraparietal sulcus (IPS) is recruited more during overall shape perception as compared to the perception of basic shape features (e.g., the degree of curvature, edge length, T-junctions) (Bodegard et al., 2001). Moreover, activation in this latter region has been found in response to haptic stimuli comprised of everyday, common objects (Amedi et al., 2001, 2002, 2005; Deibert et al., 1999; Reed, Shoham, & Halgren, 2004), as well as simple, geometrical shapes (Bodegard et al., 2001; Roland et al., 1998).

Extending beyond unisensory object recognition, there has been a significant amount of research concerning visuohaptic convergence in the LOC and the IPS. Many studies have shown that the convergence of visual and haptic inputs for object preference in adults occurs at two particular sites: the lateral occipital tactile-visual region (LOtv, located within the LOC) for object recognition, and the anterior/middle aspects of the IPS for object-directed motor actions (Amedi et al., 2001, 2002; James et al., 2002a; James & Kim, 2010; Stilla & Sathian, 2008). Several more recent studies have shown that information from vision and haptics is also combined at these sites (Kim & James, 2010;

Kim, Stevenson, & James, 2012; Tal & Amedi, 2009).

Yet, it remains unknown how and when, developmentally, multisensory information comes to converge on the LOC and the IPS. These questions can be addressed by examining the neural substrates of visual and haptic object recognition in children. This approach will also provide a window into the role of active perception and experience in this convergence. Historically, perceptual development has been conceptualized in terms of sensorimotor interactions based on the behaviors of infants and young children in tasks that require some degree of multisensory perception. For instance, as soon as infants can move their arms and hands, they are able to act on objects and receive multisensory information about those objects. As revealed by a large body of literature, these types of self-generated actions produce statistical regularities between the sensory and motor systems, and thus, play a critical role in perceptual learning (Held & Hein, 1963; James, 1890; Lungarella & Sporns, 2005, 2006; Smith, 2005). This form of active perception has been demonstrated in many behavioral studies examining the development of visual and haptic perception. For example, the development of visual perception has been shown to be highly influenced by the manner in which young children haptically explore objects (Bushnell & Boudreau, 1993; Ruff, 1984, 1986, 1989). Recent research has found increases in measures of visual object recognition in 24 month olds who demonstrate more adult-like manual exploration patterns (James et al., 2013). Additional studies examining the development of haptic perception in 4- to 5-year-old children have consistently indicated stereotypically adult-like patterns of haptic exploration by this age, as well as highly successful haptic object recognition abilities in the absence of vision (Bushnell & Baxt, 1999; Kalagher & Jones, 2011a; Lederman &

Klatzky, 1987). In spite of these achievements, however, a protracted development of visual processing of object shape in children, either behavioral or neural, may have cascading effects on the developmental trajectory of visuohaptic convergence overall.

Behaviorally, a bias for categorizing objects based on shape emerges only around 24 months of age (Jones & Smith, 2005; Pereira & Smith, 2009; Smith, 2009; Son, Smith, & Goldstone, 2008; and many others). Visual processing of object shape continues to follow this delayed trajectory, particularly for complex objects. That is, even much older children aged 6 to 8 years struggle with recognizing some complex classes of objects such as faces (Mondloch, Maurer, & Ahola, 2006; however, see Crookes and McKone, 2009), as well as objects from unusual views (Bova et al., 2007; Juttner, Muller, & Rentschler, 2006; Mondloch et al., 2003; Mondloch, Le Grand, & Maurer, 2002; for a review, see Nishimura, Scherf, & Behrmann (2009)). Further, there is evidence to suggest that tool recognition performance may also have a protracted development, becoming adult-like only during early adolescence (Bova et al., 2007; Mounoud et al., 2007). Taken together, these behavioral delays in children's visual recognition abilities, particularly of complex objects, suggest a protracted development of the occipitotemporal cortex, and specifically of the LOC.

While research investigating the neural correlates of object recognition in children is relatively scarce compared to adults, evidence suggests that the LOC is generally recruited for visual object perception in an adult-like manner in children by 5 to 8 years of age (Dekker et al., 2011; Golarai et al., 2007; Grill-Spector, Golarai, & Gabrieli, 2008; Scherf et al., 2007), and during word reading in literate children (Houdé et al., 2010; Schlaggar & McCandliss, 2007; Shaywitz et al., 2004). However, this is not to say that all

object processing is adult-like at that age. Rather, the same studies also showed that neural processing of faces and scenes (Golari et al., 2007; Scherf et al. 2007), as well as animals and objects from unusual views (Dekker et al., 2011), continued to develop throughout childhood and into adolescence. This difference in the trajectory of neural development for different classes of objects could be interpreted as due to increased experience through active perception and exploration. In this case, it suggests that object recognition in the LOC is perhaps modulated by this type of experience. Indeed, studies suggest that recruitment of this region is experience-based; findings have shown that letter stimuli activate the LOC in an adult-like way in children only after active (printing) practice, but not in children that only have visual experience (James, 2010; James & Engelhardt, 2012). Moreover, expertise with a limited class of objects such as Pokémon characters results in enhanced recruitment in several areas of the ventral occipitotemporal cortex compared to non-expert children (James & James, 2013). In sum, although the LOC is recruited during visual object recognition early on during development, its response profile appears to be continually shaped by experience. Given the limited number of studies that have investigated object processing in the LOC through development, and that they have only been done visually, it is difficult to know how and when vision converges with haptics for multisensory object recognition in this region, or even the neural substrates that underlie haptic recognition itself.

To address these gaps in knowledge, the present study aimed to: a) map out the neural systems that underlie visual *and* haptic processing of common objects in children sampled from two developmental age groups—specifically, 4 to 5.5 year olds and 7 to 8.5 year olds; and b) examine those neural systems for evidence of convergence at

different stages of development and compare them to adults. According to previous findings, children between 8 to 10 years of age begin to show adult-like behavioral patterns for visuohaptic integration and form discrimination (e.g., size and orientation; Gori et al., 2008). As this integration of form information does not become statistically optimal until 8 to 10 years (Gori et al., 2008), this indicates a developmental shift in processing prior to 8 years. Moreover, several fMRI studies have suggested that the LOC becomes adult-like between 5 to 8 years in terms of object recognition (Grill-Spector, Golarai, & Gabrieli, 2008; Golarai et al., 2007; Scherf et al., 2007), which indicates a developmental transition prior to 5 years. Given these psychophysical and neuroimaging findings, we therefore selected age groups that would capture the transitional periods for integration and recognition prior to becoming adult-like for comparison with adults.

Our hypotheses were based on contrasts between common objects and real textures to obtain a measure of object preference for both visual and haptic modalities. We predicted that the LOC and perhaps the IPS would be key regions to show developmental trends for visuohaptic convergence. Additionally, we made three specific predictions regarding the division of labor between visual and haptic object shape preference in the LOC. First, we hypothesized that visual object preference would reach adult-like levels by 5 to 8 years of age (Grill-Spector, Golarai, & Gabrieli, 2008; Golarai et al., 2007; Scherf et al., 2007), particularly due to our use of common objects. Second, though the neural development of haptic object recognition is unknown, we hypothesized that it would follow a similar trajectory as vision. Third, we predicted that visuohaptic convergence would follow a protracted development compared to vision or haptics alone. Similar to the relatively delayed development of visual recognition of over-learned or

more complex classes of objects, visuohaptic convergence of object preference may be a more complex form of processing than unisensory object preference. Just as there are subregions in the occipitotemporal cortex that process different visual object categories (e.g., faces, places), there is also a specific subregion that is involved in processing the combination of both visual and haptic object shape, namely the LOtv. It may be that this LOtv subregion has a more protracted development than the LOC proper.

2.2. Materials and methods

2.2.1. Participants

Participants were recruited from three age groups: 4 to 5.5 years (N = 15, 9 female; mean age = 4.9 years, SD = 0.5 years), 7 to 8.5 years (N = 13, 6 female; mean age = 8.1 years, SD = 0.5 years), and adults (N = 8, 3 female; mean age = 26.9 years, SD = 4.2 years). Participants had normal or corrected to normal vision, and had no known history of psychological disorders; all were healthy and met the criteria for MRI scanning. Written informed consent was obtained from the parents and adult participants, and written informed assent was obtained from the children aged 7 years or older. Parents and children were compensated with a gift certificate and a small toy; adult participants were compensated with $25. This research was approved by the Indiana University Protection of Human Participants Board.

2.2.2. Stimuli

The stimuli consisted of 8 objects and 8 textures that were explored visually and haptically. Four additional objects and textures were used during training. Stimuli were equally colorful and salient so as to maintain children's interest during the experiment,

and included objects and textures commonly found in children's environments. The objects were three-dimensional, rigid, and solid bodies that were controlled for texture such that all objects were smooth, and for size to ensure that even the 4- to 5.5-year-old children could fit both of their hands around them during haptic exploration. The textures were real, and consisted of two-dimensional square sheets to control for shape (see Table 1. for specific stimuli and dimensions). All objects and textures were photographed at a typical viewing angle against a black background to facilitate recognition during visual exploration. Participants did not see or feel the test objects or textures prior to the scan.

2.2.3. Neuroimaging procedure

After screening and obtaining informed consent, all participants were acclimated to an MRI environment. Children watched as a short cartoon was played on a screen in the MRI simulator, an artificial MRI environment with the same dimensions and sounds as the actual MRI environment. Participants were then trained in the experiment. They were instructed to lie still, and an MRI-safe lap desk was placed over their midsection. A cape was placed over their torso and arms, and was tucked under their chin. The cape covered the lap desk and allowed the participants to feel the stimuli with their hands without being able to see them. Participants were instructed to look at the stimulus presented on the screen when they saw the word "LOOK" and to feel the stimulus that was attached to the lap desk with a piece of Velcro when they saw the word "FEEL." It was explained to them that this was the procedure they would follow in the actual testing environment. Once the participants were comfortable in this setting and could perform the task efficiently, they were then introduced to the actual MRI environment.

In the MRI, participants were again given the instructions, and the lap desk and

cape were placed over their midsection. All visual stimuli were back-displayed via a Mitsubishi XL30 projector onto a screen located behind the participants in the bore of the MRI; this screen was viewed through a mirror that was placed on top of the head coil. Instructions and visual stimuli were presented using SuperLab Pro 2.0.4 software from an Apple MacBook laptop. A high-resolution anatomical scan was first acquired while participants watched a cartoon. Upon completion of this scan, the functional scans were acquired.

During the functional scans, participants were tested in a block design that involved unisensory visual exploration of 2D images of the objects and textures, and unisensory haptic exploration of the 3D stimuli. This yielded four conditions: (a) visual objects (VO); (b) visual textures (VT); (c) haptic objects (HO); and (d) haptic textures (HT). During the visual conditions, the participants viewed the stimuli presented on the screen using both eyes. During the haptic conditions, an experimenter who stood next to the participant in the MRI exchanged the objects and textures on the lap desk, and the participants explored the stimuli actively using both hands. All participants regardless of age manipulated the haptic stimuli within the scanner for the entire duration of time allotted to them. This was confirmed by the experimenter upon completion of every scan. Sixteen-second blocks of stimuli were interspersed with 10-s-long inter-block-intervals (IBIs), during which participants viewed a red fixation cross. Our experience with testing these age groups suggests that using a longer IBI increases the incidence of data loss due to excessive head motion, presumably because children lose interest during the longer interval. Furthermore, analyses of simulated data have shown that block design protocols with 10 s IBIs do not have appreciably greater statistical power than protocols with 12 s

or 14 s IBIs with signal-to-noise ratios in the range that is typical on our scanner.

Stimuli were presented sequentially for 4 s each following 2 s of instructions (Fig. 1). A single block consisted of 4 out of the 8 stimuli from each condition, and was presented twice within a given run to comprise the entire set of stimuli per condition. This resulted in 8 blocks per run, and approximately 4-min runs (118 volumes, 236 s). Trials were randomized, and blocks were counterbalanced. There were 4 functional runs administered for each participant. Due to the young age of the children, however, some runs were not completed due to fussiness or excessive motion; these runs were subsequently excluded from further analyses. Imaging sessions lasted a total of approximately 30 min. After the scanning was completed, participants were removed from the MRI environment and relocated to a controlled lab setting for behavioral testing.

2.2.4. MRI data acquisition and preprocessing

Imaging was performed with a 3-T Siemens Magnetom Trio whole body MRI system located at the Indiana University Psychological and Brain Sciences department within the Imaging Research Facility. With a phased array 12 channel head coil, whole-brain functional volumes were acquired using a gradient echo planar imaging (EPI) sequence (TE = 30 ms, TR = 2000 ms, flip angle = 70°) for BOLD-based imaging. The field of view was 192 cm with an in-plane resolution of 64x64 pixels and 33 slices per volume (3.8 mm thick with a 0 mm gap). This resulted in a voxel size of 3x3x3.8 mm. Using analysis tools in the BrainVoyager QX^{TM} 2.2 software package (Brain Innovation, Maastricht, Netherlands), functional data underwent slice scan-time correction, 3D motion correction, linear trend removal, and Gaussian spatial blurring (FWHM 6mm). High-resolution T1-weighted anatomical volumes (resolution: 1.5 mm^3, 120 sagittal

slices) were acquired using a 3-D Turbo-flash inversion recovery sequence prior to the functional imaging. By applying an intensity-matching, rigid-body transformation algorithm, individual functional volumes were co-registered to the anatomical volumes. Both anatomical and functional volumes were normalized to a standard space using an affine transformation based on the 8 parameters of the Talairach reference (Talairach & Tournoux, 1988). During normalization, voxels of the functional volumes were resampled to 3 mm^3.

2.2.5. Data analysis procedures

All of the functional data were entered into separate random-effects general linear models (GLM), one for each age group, in BrainVoyager QX™ 2.2. Predictors in the design matrix were based on the blocked stimulus presentation timing across runs and across participants, and were convolved with a two-gamma impulse response function. Motion parameters for each run for each participant were included in the design matrix as predictors of no interest. Functional runs with motion estimates exceeding 5 mm on any axis were excluded from the analyses. Although this is a more liberal threshold than is often used in studies with only adults, it was adopted here because a stricter criterion would have eliminated many of the child participants, thus reducing the practical utility of the procedure. While there may be concerns regarding this threshold and its impact on the data, a further analysis of motion artifacts revealed no significant correlations between head motion and BOLD signal change. These data are presented in Supplementary materials. This criterion resulted in a total of 36 usable runs (on average, 2.4 runs per participant) for the 4- to 5.5-year-old children, 45 runs (3.5 runs per participant) for the 7- to 8.5-year-old children, and 32 runs (4 runs per participant) for the

adult group.

For the group-defined region-of-interest (ROI) analyses, multisensory object-selective regions, particularly the LOC and the IPS, were functionally localized by contrasting visual objects with visual textures, in conjunction with haptic objects over haptic textures (i.e., (VO > VT) ∩ (HO > HT)). These regions were defined across all participants in the three groups (N = 36) so as not to commit the egregious error of "double-dipping" (Kriegeskorte et al., 2009). BOLD signal change was measured in the same voxels across all participants to limit the bias of selecting different neural substrates, but the potential downside to this method is that individual participants may overlap with the group-defined ROIs to different degrees. Therefore, to assess the appropriateness of using group-defined ROIs, two additional analyses were performed: 1) the variability in location of the individual ROIs was measured across the three age groups; and 2) individually-defined ROIs were examined for comparison. These analyses are presented in more depth in subsection *2.3.4. Results of individual-based ROI analyses*, as well as in Supplementary materials.

Estimates of the BOLD signal change as beta weights were extracted for each condition for each participant using the BrainVoyager ROI/VOI-ANCOVA table tool. Statistical hypothesis testing on these BOLD signal change values was performed using repeated measures analyses of variance (ANOVA) in SPSS.

In addition to the ROI analyses, supplementary whole-brain analyses were performed. Whole-brain statistical parametric maps (SPMs) were calculated for each group using GLMs. Specific contrasts were performed within each group to assess multisensory shape-selectivity (a conjunction: (VO > VT) ∩ (HO > HT)), and unisensory

shape-selectivity (VO > VT; HO > HT). These contrasts were thresholded with a voxel-wise *p*-value of 0.01 per map and corrected for multiple tests using a permutation test. This resulted in a cluster threshold of at least 11 contiguous voxels for the conjunction contrast, and at least 21 voxels for the simple contrasts. Furthermore, conjunction contrasts were thresholded using an alpha-level of .05; simple contrasts were thresholded using the square root of the threshold used for the conjunction contrast, which resulted in an alpha-level of .22. This was done to facilitate comparisons of overall activation between the three contrasts such that activation from the conjunction threshold would overlap with the simple contrasts.

2.2.6. Post-scan crossmodal behavioral test procedure

To examine recognition ability, participants were behaviorally tested in two blocks of crossmodal haptic-to-visual 8-alternative-forced-choice match-to-sample tasks, including one block of objects and another of textures. Participants were first instructed to place their hands inside a box with two circular openings, one for each hand. A laptop screen displaying an array of the same 8 objects or textures from the fMRI portion was placed on top of the box. A black felt sheet covered the laptop keyboard and the box so that the participants could feel, but not see, the stimulus. Objects and textures were placed inside the box one at a time for 5 s of haptic exploration. Participants were then instructed to remove both of their hands from the box, and within 5 s, to point to the matching visual stimulus out of the 8-alternative array. This was ample time for all of the groups to perform the task. Each object and texture was presented inside the box only once, and the order of blocks was counterbalanced among participants. Upon completion of this task, participants were compensated for their time.

Responses for the behavioral 8-alternative-forced-choice match-to-sample task were coded during the experiment by a second experimenter, and were later analyzed for successful recognition. This was calculated as a proportion for objects and for textures by taking the number of correctly identified matches over the total number of trials per block. Chance performance was at 12.5%, or 1 out of 8, in selecting the correct match from the array of 8 stimuli. These proportions were then averaged within each group and compared using a repeated measures analysis of variance (ANOVA) in SPSS.

2.3. Results

2.3.1. Functional ROI results

To investigate the development of function in the brain regions previously implicated in visuohaptic object preference, regions of interest were defined using the data from all age groups and a contrast of visual objects versus visual textures in conjunction with haptic objects versus haptic textures (Fig. 2). Two bilateral visuohaptic object-preferring regions were localized in this way (Table 2). The ventral occipital region was located near the previously reported coordinates of the LOtv. The dorsal parietal region, rather than being near the coordinates of previously reported anterior or middle IPS (aIPS/mIPS), was instead closer to caudal IPS (cIPS). While this region has been reported in studies of adult visual object recognition (Faillenot et al., 1997; James et al., 2000, 2002b; Kraut et al., 1997), it is only rarely found during adult haptic object recognition (Peltier et al., 2007; Stilla & Sathian, 2008). Nevertheless, our results showed that this region was also active in children during haptic object recognition.

The main hypotheses were tested with a 2x2x3 repeated measures ANOVA with BOLD signal change (beta weights) as the dependent variable, stimulus type (objects and textures) and sensory modality (vision and haptics) as the within-subjects factors, and age group (4 to 5.5 year olds, 7 to 8.5 year olds, and adults) as the between-subjects factor. The patterns of activation in the left and right hemispheres were similar for the LOtv and cIPS, which was to be expected as many studies have consistently found bilateral activity for visuohaptic object preference (Amedi et al., 2001, 2002; Saito et al., 2003; Zhang et al., 2004). Yet, it is important to note that previous studies have also reported laterality effects—some have shown what appear to be weaker signals in the right than in the left hemisphere (Kim & James, 2010; Kim, Stevenson, & James, 2012), while others have found task-dependent lateralization in the LOC (Large, Aldcroft, & Vilis, 2007). As such, the issue of laterality remains complex (for a brief, but pertinent discussion of the lateralization of visual and haptic processing, see Stilla & Sathian (2008)). Given our data, however, the effects seemed to be bilateral and were consequently collapsed across hemisphere for each region.

The results from the complete design for the two ROIs are shown in Fig. 3A-B. Results in the LOtv indicated a main effect of age group ($F(2,33) = 10.41$, $p < .001$, $MSe = 2.11$), and of stimulus type ($F(1,33) = 54.41$, $p < .001$, $MSe = 3.80$) with a greater response for objects than textures ($t(35) = 5.69$, $p < .001$). Modality, however, was not a significant main effect. Additionally, there was a significant stimulus type by age group interaction ($F(2,33) = 6.15$, $p < .005$, $MSe = .43$). This interaction is shown in Fig. 4A with the data collapsed across modality. Post-hoc *t*-tests revealed a developmental trajectory of increasing BOLD activation with objects across age; BOLD activation with

objects was significantly greater in the 7- to 8.5-year-old children than in the 4- to 5.5-year-old children ($t(26) = 2.29$, $p < .05$), and significantly greater in adults than in 7 to 8.5 year olds ($t(19) = 3.48$, $p < .01$). Results in bilateral cIPS showed a main effect of stimulus type ($F(1,33) = 31.63$, $p < .001$, $MSe = 2.01$) in favor of objects over textures ($t(35) = 3.34$, $p < .01$). Similar to the findings in bilateral LOtv, there was a significant stimulus type by age group interaction ($F(2,33) = 5.73$, $p < .01$, $MSe = .37$; Fig. 4B). Post-hoc *t*-tests revealed increasing activation with objects between the 4 to 5.5 year olds and the adults ($t(21) = 3.05$, $p < .01$). Other key results were differences in activation for visual objects between adults and 4- to 5.5-year-old children (LOtv: ($t(21) = 4.20$, $p < .001$); cIPS: ($t(21) = 3.48$, $p < .01$)), and between adults and 7- to 8.5-year-old children (LOtv: ($t(19) = 3.98$, $p < .001$); cIPS: ($t(19) = 2.63$, $p < .05$); Fig. 3A-B).

To examine further the developmental increase in activation with objects, object preference was calculated as the difference between BOLD activation with object stimuli and texture stimuli for both vision and haptics (i.e., VO > VT; HO > HT) in the LOtv and cIPS (Fig. 5). Significant visual object preference was found in adults (LOtv: ($t(7) = 9.50$, $p < .001$); cIPS: ($t(7) = 5.38$, $p < .001$)), and in the 7- to 8.5-year-old children (LOtv: ($t(12) = 4.47$, $p < .001$); cIPS: ($t(12) = 2.11$, $p < .05$)). Haptic object preference was also significant in adults (LOtv: ($t(7) = 4.29$, $p < .01$); cIPS: ($t(7) = 4.26$, $p < .01$)), and in 7 to 8.5 year olds (LOtv: ($t(12) = 2.61$, $p < .05$); cIPS: ($t(12) = 2.29$, $p < .05$)). In the LOtv (Fig. 5A), adults showed significantly greater visual preference than the 4- to 5.5-year-old children ($t(21) = 3.67$, $p < .01$), and the 7- to 8.5-year-old children ($t(19) = 4.24$, $p < .001$). Haptic preference, however, was not reliably different among the three groups in any of the ROIs. As a result, adults demonstrated a significant difference between visual

and haptic object preference ($t(7) = 4.57$, $p < .01$), but children did not. In bilateral cIPS (Fig. 5B), visual object preference followed the same pattern as in the LOtv. That is, adults showed greater activation for visual object preference than the 4- to 5-year-old children ($t(21) = 3.42$, $p < .01$), and the 7- to 8.5-year-old children ($t(19) = 3.54$, $p < .001$). Overall, these statistical effects did not appear to be driven solely by the adult activation pattern as the 7 to 8.5 year olds demonstrated significant BOLD activation with visual and haptic object stimuli above baseline, as well as significant levels of object preference.

2.3.2. Results from whole-brain contrasts

Whole-brain contrasts were performed to supplement the ROI analyses and obtain a more global perspective of the activation patterns that may be changing over the course of development. The results of a conjunction contrast assessing visuohaptic object preference (i.e., (VO > VT) ∩ (HO > HT)) in adults are shown in Fig. 6. As expected, adults showed bilateral bimodal visuohaptic object preference in regions previously indicated in the literature, including both the LOC and anterior/middle aspects of the IPS. The same conjunction contrast performed in the two groups of children yielded no significant clusters. However, a direct comparison of children and adults with the same contrast similarly produced no significant clusters. Combined with the results of the ROI analysis, these findings suggest that children activate a similar set of brain regions as adults, but with perhaps sub-threshold signal levels or higher variability.

Results from the unisensory visual preference contrast (VO > VT) revealed both the LOC and the IPS as significantly activated bilaterally in adults (Fig. 7). The two groups of children showed activation in the LOC that overlapped with adults. However,

in both groups, the cluster was only found in one hemisphere—the left hemisphere in 4- to 5.5-year-old children, and the right hemisphere in 7- to 8.5-year-old children. Neither group of children showed a significant cluster in the IPS.

In the unisensory haptic object preference contrast (HO > HT), adults showed significant bilateral activity in the LOC and the IPS. Neither group of children showed significant clusters in the LOC. Instead, 4 to 5.5 year olds showed a significant cluster in the right postcentral gyrus, and 7 to 8.5 year olds showed a significant cluster in the right caudal IPS (cIPS) area, which also overlapped in part with the same cIPS area in adults (Fig. 8).

2.3.3. Behavioral results from the crossmodal matching task

Results from a 2 (stimulus type: objects and textures) x 3 (age group: 4 to 5.5 year olds, 7 to 8.5 year olds, and adults) repeated measures ANOVA with behavioral performance as the dependent variable showed significant main effects of stimulus type ($F(1,33) = 28.23$, $p < .001$, $MSe = 1.12$), and age group ($F(2,33) = 13.73$, $p < .001$, $MSe = .63$), as well a significant stimulus type by age group interaction ($F(2,33) = 3.69$, $p < .05$, $MSe = .15$). Post-hoc *t*-tests comparing proportional success within each group indicated greater success for objects than for textures (Adults: ($t(7) = 3.21$, $p < .05$); 7 to 8.5 years: ($t(12) = 2.94$, $p < .05$); 4 to 5.5 years: ($t(14) = 4.77$, $p < .001$)). Between groups, there were no significant differences with regard to objects; performance was either at or near ceiling in all groups. Comparisons of matching success on textures, however, indicated differential proportions of success (Fig. 9). The group of 4 to 5.5 year olds performed worse than 7 to 8.5 year olds ($t(26) = 3.75$, $p < .001$), and adults ($t(21) = 4.20$, $p < .001$), but the 7 to 8.5 year olds did not differ significantly from adults ($t(19) = 0.95$, $p =$ n.s.).

2.3.4. Results of individual-based ROI analyses

One important concern for using group-based functional regions-of-interest (ROIs), particularly across different developmental populations, is that the variability of overlap between individual ROIs and the group ROI may be different. Several studies have demonstrated that children show a more diffuse pattern of activation than adults (e.g., Casey, Galvan, & Hare, 2005; Durston et al., 2006; Stiles et al., 2003; however, see commentary by Brown, Petersen, & Schlagger (2006)). Thus, lower activation for children as compared to adults in a group-based ROI could be due to less overlap of individual ROIs with the group ROI rather than to a true decrease in BOLD signal. To allay this concern with respect to our findings, we performed two analyses. First, the variability in terms of the location of individual ROIs (i.e., ROI variability) was examined in the three age groups. This analysis—the results of which are reported below—served to explore further the development of neural substrates for visuohaptic processing by examining ROI variability as an additional dependent variable. Second, an analysis of individually-defined ROIs was performed for comparison with the group-defined ROI analysis. These results are reported in the supplementary materials as the individual-based BOLD ROIs indicated similar patterns and confirmed the primary findings from the group-based ROIs.

The analysis of individual ROI variability was conducted by implementing a multistep process. First, the four ROIs (i.e., left and right LOC and IPS) were identified in each participant using the conjunction contrast (i.e., (VO > VT) ∩ (HO > HT)). For participants who did not produce a significant cluster in the approximate location of the ROI at the standard FDR threshold, the statistical threshold was lowered until a cluster of

at least 2 voxels appeared. This technique was used to ensure that variability was measured across the entire sample, and not just the participants that had the highest levels of BOLD contrast. The locations of the center of mass in Talairach coordinates for each cluster were then extracted (Talairach & Tournoux, 1988). Second, for each of the three age groups and each of the four ROIs, a prototypical ROI center was calculated as the mean center of mass across participants. Third, the Euclidean distance from the center of each participant's ROI to the prototypical ROI center was measured (in mm). Mean absolute distances were used to assess the variability around each prototypical ROI center. Finally, a 3 x 4 repeated measures ANOVA was performed with the Euclidean distance from the mean (mm) as the dependent measure, ROI (left LOC, right LOC, left IPS, and right IPS) as the within-subjects factor, and age group (4 to 5.5 year olds, 7 to 8.5 year olds, and adults) as the between-subjects factor.

The results of the variability analysis indicated a significant main effect of age group ($F(2,33) = 14.87$, $p < .001$, $MSe = 4467.84$). For all four ROIs, 4 to 5.5 year olds showed greater spread of ROI location (i.e., greater variability) than 7 to 8.5 year olds and adults (Fig. 10). No other effects were significant.

The analyses of BOLD signal change suggested that the part of the LOC most involved in visuohaptic convergence (i.e., the LOtv) continues to develop beyond 8 years of age. Can these results be explained instead by differences in ROI location variability? Our analysis of variability did show significant differences across groups; however, this pattern of differences in variability did not match the pattern of differences in BOLD signal change. Specifically, the results of the variability analysis showed a separation between 4 to 5.5 year olds and the older 7 to 8.5 year olds as well as adults, whereas the

findings with BOLD signal change showed a separation between adults and both groups of children. Thus, the results of BOLD signal change cannot be explained by differences in variability. One of our expectations was that BOLD signal change in the LOtv would show changes not only between children and adults, but also between younger and older children. The findings of BOLD signal change showed little evidence for this pattern. However, it is interesting to speculate that the decrease in variability of ROI locations from 4 to 5.5 year olds to 7 to 8.5 year olds may reflect the development (and perhaps consolidation) of visuohaptic convergence. As such, this pattern of variability must be taken into consideration for future studies because it could explain possible differences in BOLD signal change in children from 4 to 8.5 years.

2.4. Discussion

Object recognition is ubiquitous, complex, and crucial for interacting with the environment. It has been extensively documented that the LOC is critical for visual object recognition and that BOLD activation in this region is related to recognition performance (Grill-Spector, Kushnir, Hendler, & Malach, 2000; Grill-Spector et al., 2001; James et al., 2002a, 2002b; James et al., 2000; see Grill-Spector et al. (2008) for a review). Furthermore, a subregion of the LOC, the LOtv, is well-known to be involved in both visual and haptic object recognition in adults (Amedi et al., 2002; James et al., 2002b; James & Kim, 2010; James, Kim, & Fisher, 2007; Stilla & Sathian, 2008). However, one important factor in understanding the organization of the brain is to understand its development. To our knowledge, this is the first known study to track the neural development of the LOC in children as young as 4 years of age, and during a haptic task.

The results of the current study showed a developmental increase in visual object preference—defined as a preference for objects over textures—in the LOtv that did not reach adult-like levels by 8.5 years of age. This finding is different from previous reports that object preference in the LOC as a whole reaches adult-like levels sometime between 5 and 8 years of age (Golarai et al., 2007; Scherf et al., 2007). The current results further demonstrated a dissociation between the developmental trajectories of visual and haptic object preference in the LOtv, with adult-like haptic preference reached earlier than visual preference. Taken together, these findings suggest that: (1) the development of the LOtv subregion is more protracted than the LOC proper; and (2) the division of labor between visual and haptic object shape processing in the LOtv is relatively equivalent early on in development, but becomes visually dominant sometime between 8.5 years and young adulthood.

Based on previous research, we initially hypothesized that visual object preference would be adult-like across all three groups of participants in the LOtv subregion. However, the results indicated a developmental increase in visual object preference in this area. As such, these results may be inconsistent with findings from previous studies indicating early maturation of the LOC for object-processing (Scherf et al., 2007; Golarai et al., 2007). In these studies, the processing of real, common, and colorful moving objects was reported to be comparable to adults by 5 to 8 years (Scherf et al., 2007), and the processing of novel, abstract, and gray-scale static objects was also found to be comparable to adults by 7 to 11 years (Golarai et al., 2007). Thus, the discrepancy between the current and previous results may be attributed to the use of different stimuli or to the differences in the binning of age groups. A more likely

alternative is that the previous studies measured activation from the LOC "proper," whereas the current study measured from the LOtv subregion. This difference in specificity may be similar to the difference in developmental timelines for the LOC proper versus the relatively protracted responses of particular regions within the occipitotemporal cortex for specific object categories (e.g., faces, places, animals, and objects from unusual views). Analogous to the protracted development of visual recognition of complex classes of objects, particularly those from unusual views, visuohaptic object recognition may also be delayed relative to visual or haptic object processing in terms of viewpoint independence. Crossmodal studies in adults have found visuohaptic object representations to be view-independent, arising from the integration of view-dependent, unisensory (visual and haptic) modalities; further, these more complex, multisensory representations appear to reflect spatial transformation abilities (Lacey et al., 2009; Lacey, Peters, & Sathian, 2007). Therefore, it seems likely that visuohaptic object processing requires more specialization or fine-tuning than either visual or haptic object processing alone, and that visual object processing in the LOtv may require more experience to develop fully. Our results indicate that full development occurs sometime between 8 years and young adulthood, which is consistent with previous psychophysical findings of visuohaptic integration suggesting that form perception does not become optimal until after 8 years (Gori et al., 2008).

Given that exploratory interactions in children may be restricted by their relatively limited experience, it is conceivable that this restriction results in neural processing that emphasizes different types of sensory inputs. As implicated in the developmental literature, infants and children interact with objects and gain multisensory

experience as soon as they are able to move their hands. This rapid acquisition of coordination is crucial for producing statistical regularities between the sensory and motor systems and for the development of perceptual learning (Held & Hein, 1963; James, 1890; Lungarella & Sporns, 2005, 2006; Smith, 2005). Early integration of object properties from both vision and haptics aids in this development. However, as children age and gain experience, they may become more and more reliant on visual information, which results in the gradual separation between vision and haptics in the division of labor for object recognition. It is possible that the results shown here reflect this hypothetical developmental trend for young children to shift their emphasis from haptics to vision as they mature.

The increase in visual object preference through development in the LOC was paralleled by the results in the IPS. On the caudal aspect of this bilateral dorsal region (cIPS), adults demonstrated a visual dominance in object preference as compared to children, while haptic object preference did not change significantly between 4 years and adulthood. This region, considered to be homologous with the same area cIPS in the monkey (macaque) cerebral cortex, has been previously associated with the analysis of the structure of three-dimensional objects (Culham, Cavina-Pratesi, & Singhal, 2006; James et al., 2002b; Sakata et al., 1997; Shikata et al., 2003). Further, there is considerable neural evidence suggesting that this region is involved in visual object processing (Faillenot et al., 1997; James et al., 2000, 2002b; Kraut et al., 1997; Stilla & Sathian, 2008). However, the cIPS is rarely found in relation to haptic object processing (Peltier et al., 2007; Stilla & Sathian, 2008); instead, studies usually find visuohaptic preference in the anterior and/or middle IPS, which are well-known areas of neuronal

convergence (Amedi et al., 2001, 2002; James & Kim, 2010; Stilla & Sathian, 2008). More recent evidence has indicated that the left cIPS is recruited during spatial processing, specifically for locating object parts (Sathian et al., 2011). The interplay between visuohaptic object shape and location perception suggests the possibility of a multisensory neuronal pool, which forms a link connecting the processing of spatial relations between object parts and the subsequent processing of global object shape in the cIPS (Sathian et al., 2011; Stilla and Sathian, 2008). In the current study, both children and adults showed visuohaptic preference in the cIPS; and while adults showed recruitment of the aIPS, the children did not. Thus, this is the first study to demonstrate reliable object preference in the cIPS in children, and the first to suggest that object preference in the aIPS may develop later than in the cIPS. In the adult primate (macaque) brain, the cIPS sends projections to the AIP, the homologue of the human aIPS (Culham, Cavina-Pratesi, & Singhal, 2006; Sakata et al., 1997). Perhaps these projections also form in humans during development, but possibly not by 8.5 years of age. Clearly, questions such as these could be further elucidated with studies of structural and functional connectivity across development.

At the whole-brain level, the network of regions shown by children closely approximates those demonstrated by adults. Generally, the two groups of children appeared to recruit similar sensory systems as adults for visual and haptic object processing with overlapping ventral regions in the LOC and dorsal regions in the IPS, although there were some differences in the location of maximal brain activation. Children at different stages of development may be recruiting different subregions within the LOC and IPS, thus resulting in variable activation patterns, although these patterns

tended to overlap with adult activity. Even in adults, however, many studies have indicated different areas of the LOC for object recognition (Amedi et al., 2001, 2002; James et al., 2002b; Pietrini et al., 2004; Prather, Votaw, & Sathian, 2004; Reed, Shoham, & Halgren, 2004; Stoesz et al., 2003), as well as different aspects along the IPS (e.g., aIPS and mIPS) that activate during haptic exploration of objects (Binkofski et al., 1999; Bodegard et al., 2001; Culham & Kanwisher, 2001; Grefkes et al., 2002; James & Kim, 2010; Peltier et al., 2007; Roland et al., 1998; Zhang et al., 2004). While these distinctions are fairly well documented in adults, they are not so in children. In the current study, the differences in activation were predominantly reflected in the varying whole-brain response profiles shown during unisensory visual and haptic object preference as compared to the (lack of) response shown during visuohaptic convergence in children. The development of object preference in these systems did not follow an increasing trajectory of activation in the same location from younger to older children, but rather included shifts in location (e.g., between hemispheres). The resultant lack of overlap in activation in the two groups of children indicates that the development of visual and haptic convergence for object processing is not an age-dependent, additive amalgamation of individual unisensory modalities. Instead, the shifts in location likely signify a change in the strategy used for object processing. In children, slight differences in the recruitment of cognitive functions may in turn recruit different neural substrates. Due to the complexity of combining two sensory modalities, there may another factor, namely experience, that is contributing to these subtle shifts in activation for unisensory object preference. Nevertheless, the existent overlaps in activity between the adults and each of the groups of children reveal that neural processing does not move drastically in

terms of location over the course of sensory development, but instead, provides evidence that maturity within the same system may stem from increased experience.

It could be argued that texture perception and recognition is more difficult for young children than adults. Despite efforts to select texture stimuli that would be familiar to all participants, it is clear from post-experiment debriefing that children had more difficulty naming the textures than adults. This could have contributed to their poorer performance as measured by behavioral accuracy during the crossmodal haptic-to-visual match-to-sample task. Children from 4 to 5.5 years of age performed significantly worse than 7 to 8.5 year olds and adults at crossmodal matching and recognition of textures. Yet, their recognition of objects was not significantly different from adult performance, and the fact that texture recognition across the visual and haptic modalities was more difficult did not have any differential effect on neural activity. As indicated by the ROI analyses in the LOC and IPS when collapsed across modalities, there were no significant group differences with regard to texture processing; this suggests that the use of real textures acts as an appropriate control condition. Presumably, if texture recognition is more difficult and object processing is easier, then neural activity for textures would increase over the course of development while activity for objects would not change. However, we have obtained the opposite effect: BOLD signal change increased for objects over time, but remained relatively stable for textures. One possible explanation for our effects may be due to the use of realistic textures instead of scrambled objects. While most of the developmental neuroimaging literature has made comparisons between intact objects and scrambled images of those objects (Golorai et al., 2007; Scherf et al., 2007), these comparisons may only be relevant in unisensory visual studies. Research

examining haptic or visuohaptic object recognition necessitates the use of haptically recognizable textures to be contrasted with objects (Amedi et al., 2001). While both scrambled images of objects and realistic textures can be placed within a class of objects that lack characteristic shape, yet are perceptually differentiable, it is likely that only realistic textures can be haptically recognized and identified (although this remains to be tested empirically). As this is the first known study to examine haptic processing at a neural level in young children, the relation between the effects of different types of textures was difficult to predict. It is possible that the comparison between common objects and realistic textures would simply decrease object preference, and would result in less widespread activity. This, however, would only yield more conservative results relative to comparisons with scrambled objects. Nevertheless, the BOLD activity with textures seems to remain fairly stable across development and activate many of the same areas as the visual and haptic object conditions contrasted with rest. These findings, in concert with the lack of developmental change in haptic object preference, suggest that it is the development of object recognition abilities, and in particular visual object recognition rather than texture recognition, that drives the relative increase in object preference.

In summary, we have measured the neural systems of children at different ages, including those several years younger than reported in the literature, and have shown the developmental trajectories of the LOC and the IPS for visual and haptic object recognition. The present research provides evidence that the LOC, and the LOtv specifically, is indeed involved in visuohaptic object recognition early on, though it becomes increasingly visually dominant over the course of development. Additionally,

this is the first known study to show caudal IPS recruitment during haptic object recognition in both adults and children. Disparate overlapping activity between children and adults in the LOC and the IPS suggests that object preference does not develop in an additive manner from early unisensory visual and haptic convergence of information. Taken together, we conclude that the development of multisensory visuohaptic neural substrates for object recognition is protracted compared to more unisensory substrates, possibly because adult-like connectivity among these substrates requires extensive experience through active perception and exploration.

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Table 1. Stimuli and dimensions of objects and textures. * Denotes training stimuli.

Objects		**Textures**	
	Dimensions *(l x w x d* in cm*)*		Dimensions *(l x w* in cm*)*
Eraser	6.0 x 1.5 x 2.0	Sponge	10.5 x 10.5
Ball	4.5 x 4.5 x 4.5	Feathers	10.5 x 10.5
Cup	7.5 x 4.5 x 4.5	Felt	10.5 x 10.5
Star	4.5 x 4.5 x 2.0	Scrubber	10.5 x 10.5
Whistle	13.5 x 1.5 x 1.5	Corkboard	10.5 x 10.5
Sunglasses	12.0 x 4.0 x 2.5	Plastic sheet	10.5 x 10.5
Plate	11.5 x 11.5 x 1.5	Fake fur	10.5 x 10.5
Crayon	10.0 x 1.0 x 1.0	Drawer liner	10.5 x 10.5
Ice cream cone*	11.0 x 4.0 x 4.0	Paper*	10.5 x 10.5
Toothbrush*	12.5 x 2.0 x 1.5	Aluminum foil*	10.5 x 10.5

Table 2. Talairach coordinates (*x*, *y*, *z*), peak *t*-values, *p*-values, and number of voxels for visuohaptic object-preferring regions.

Region	*x*	*y*	*z*	*t*(35)	*p*-Value	No. of voxels
L LOtv	-47	-61	-12	3.31	.002	908
R LOtv	49	-65	-10	3.54	.001	1384
L cIPS	-21	-77	41	3.39	.002	217
R cIPS	25	-76	32	3.37	.002	886

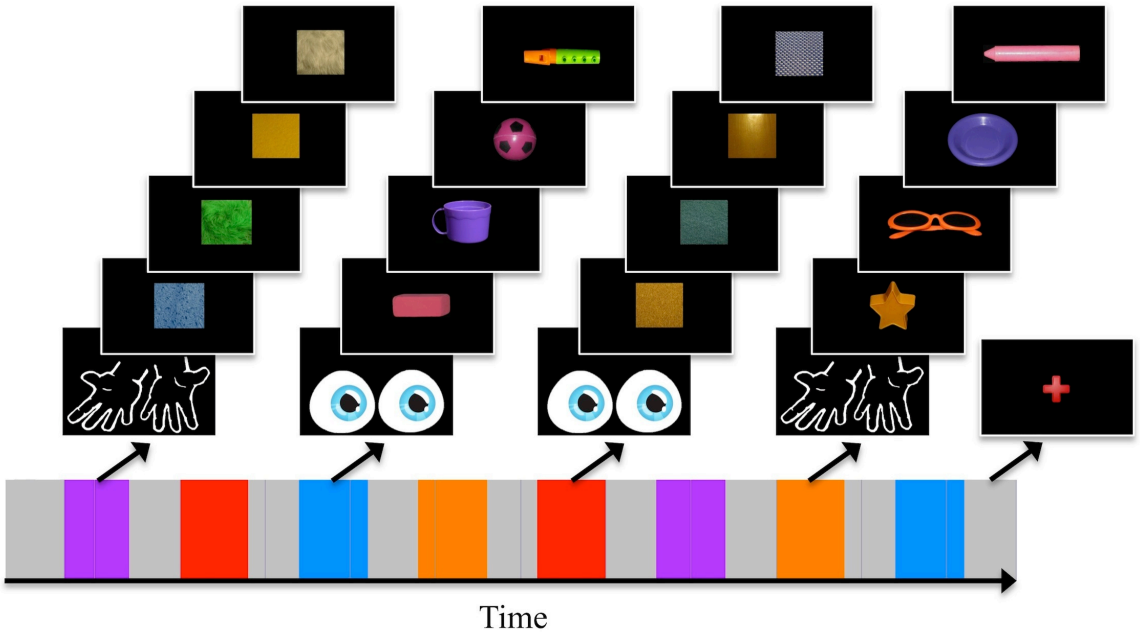

Figure 1. Graphical depiction of the fMRI block design. One sample run and stimuli used in the present study. The four conditions consist of visual objects (blue), visual textures (red), haptic objects (orange), and haptic textures (purple).

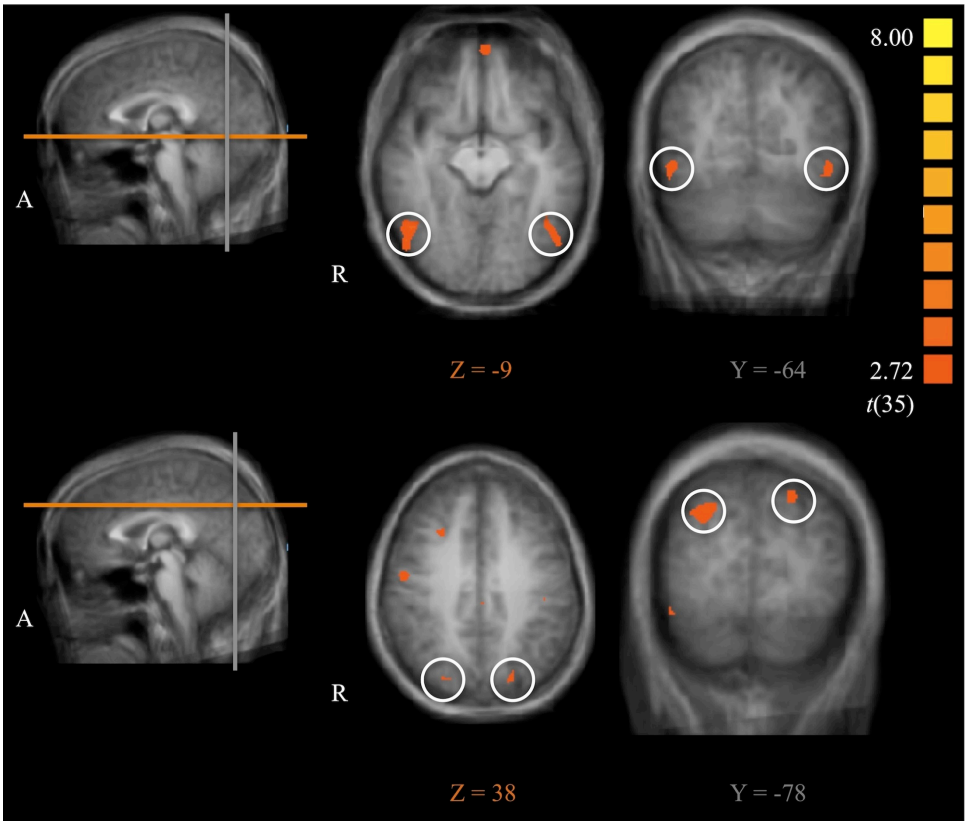

Figure 2. Multisensory object preference (VO > VT ∩ HO > HT) in all participants (N = 36). Statistical parametric map (SPM) is presented at a threshold of $p < 0.01$ (uncorrected). This contrast was used to obtain the group-defined ROIs (white circles) in bilateral LOC, namely LOtv (top row), and in bilateral caudal IPS (bottom row). Functional data are presented on an averaged human brain. On this and other figures, lines on the sagittal plane correspond to axial slices along the z-axis and coronal slices along the y-axis. A = anterior; R = right.

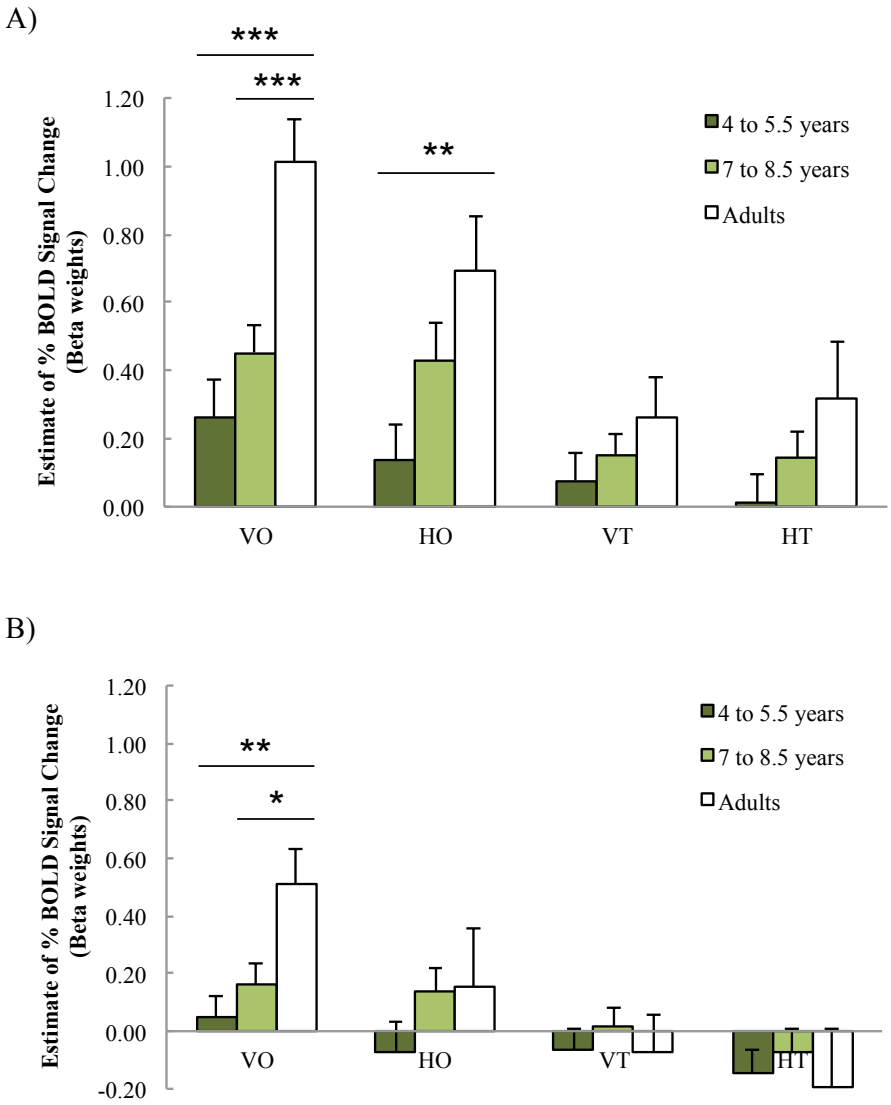

Figure 3. BOLD signal change of the complete design in bilateral LOC (A) and IPS (B). On this and subsequent figures, * denotes $p < .05$, ** denotes $p < .01$, *** denotes $p < .001$. Error bars represent SEM.

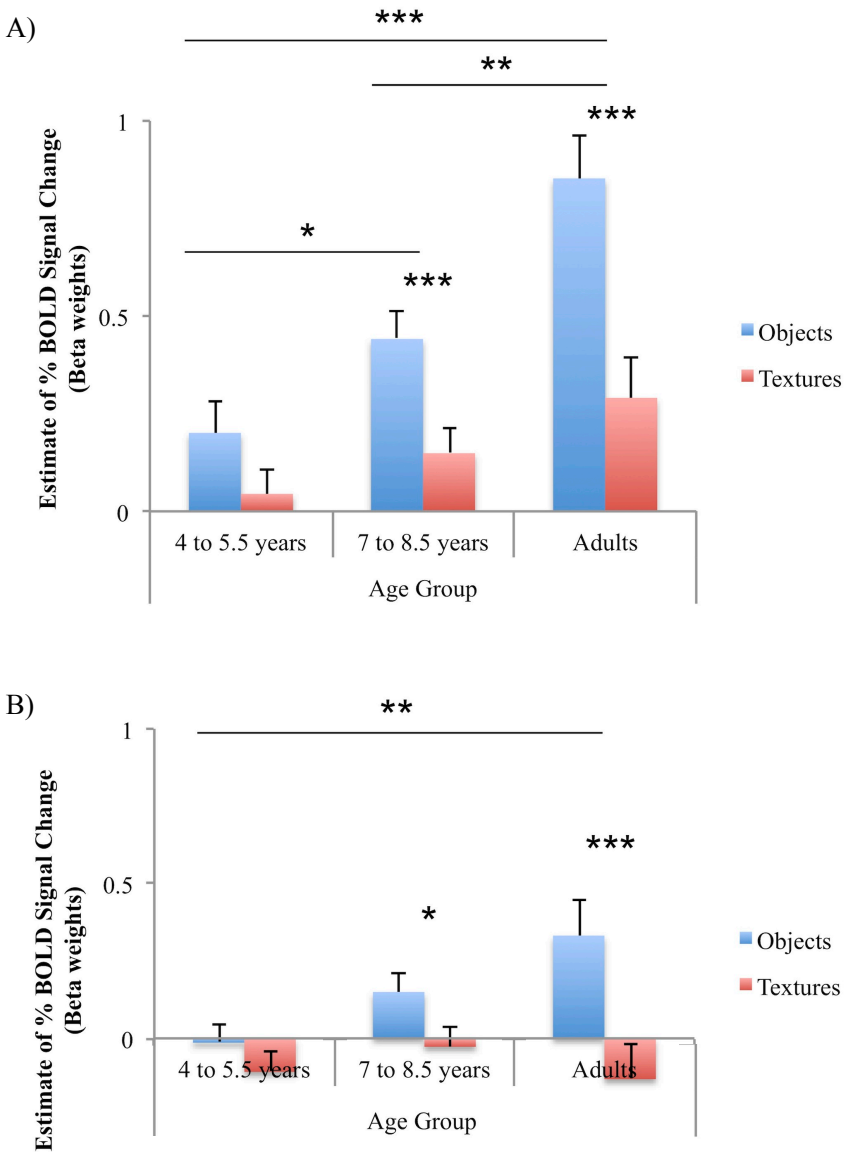

Figure 4. Objects compared to textures by age. BOLD signal change is shown as a function of age group and stimulus type collapsed across modality (i.e., VH objects, VH textures) in bilateral LOC (A) and IPS (B).

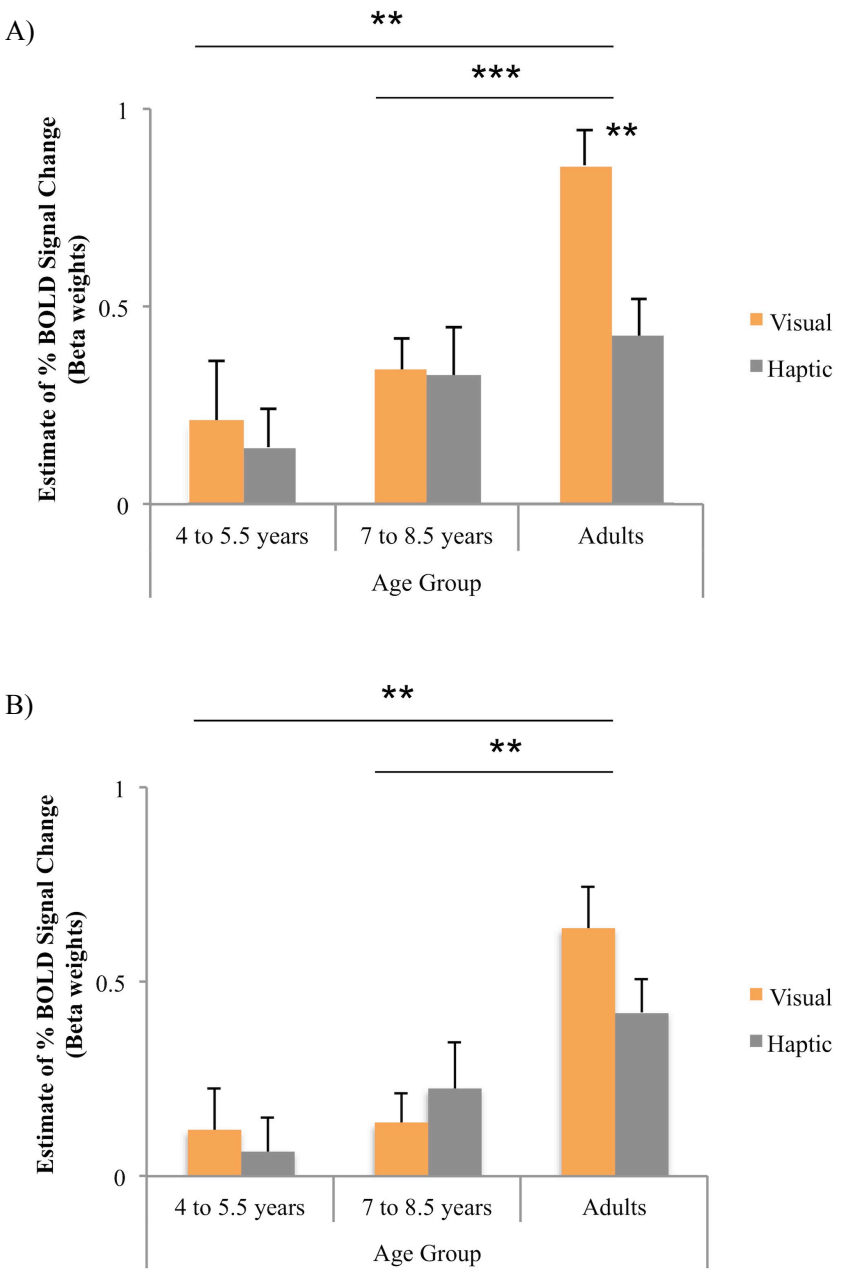

Figure 5. Visual object preference compared to haptic object preference by age. BOLD signal change is shown as a function of age group and object preference (i.e., objects > textures) by modality in bilateral LOC (A) and IPS (B).

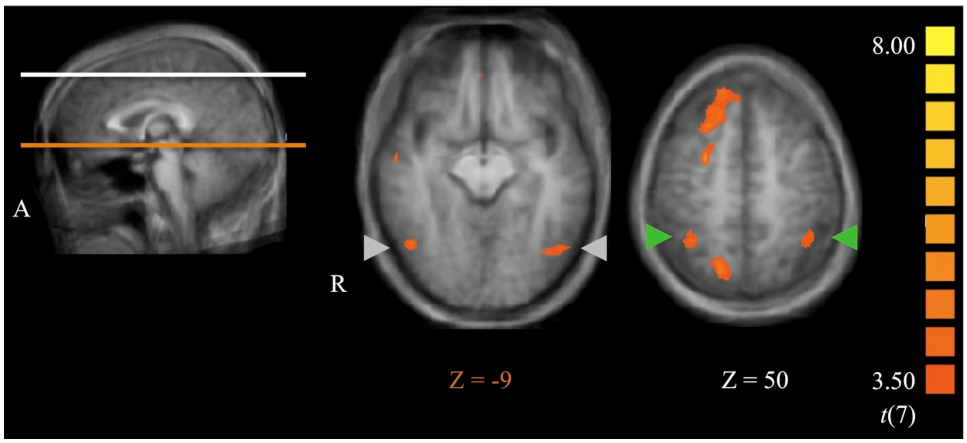

Figure 6. Multisensory object preference (VO > VT ∩ HO > HT) in adults. Group maps of averaged adult data are presented at a threshold of $p < 0.05$ (corrected). Activations are located bilaterally in the LOC (gray arrows) and in the IPS (green arrows). No clusters of activity in either group of children passed the significance threshold.

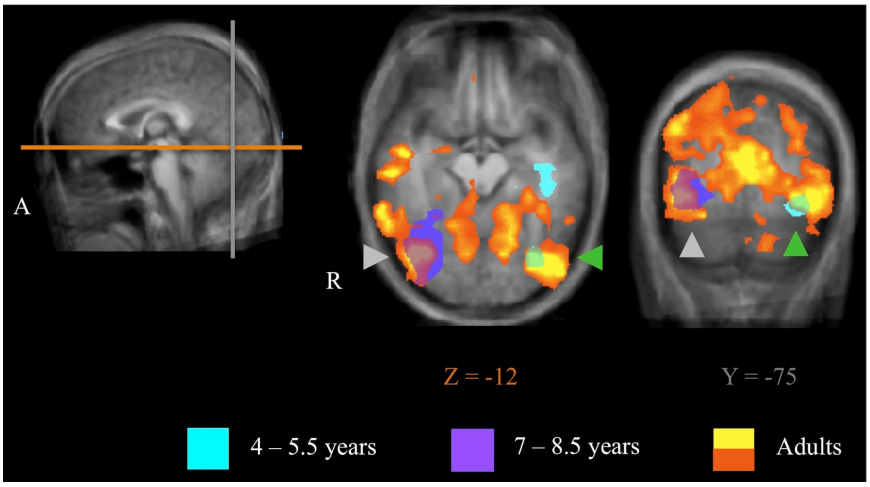

Figure 7. Visual object preference (VO > VT). Group maps are presented at a threshold of $p < 0.05$ (corrected). Overlapping activations between groups are located in the left LOC (green arrow) and the right LOC (gray arrow). Blue denotes the group of 4 to 5.5 year olds, purple denotes the group of 7 to 8.5 year olds, and orange/yellow denotes the adult group.

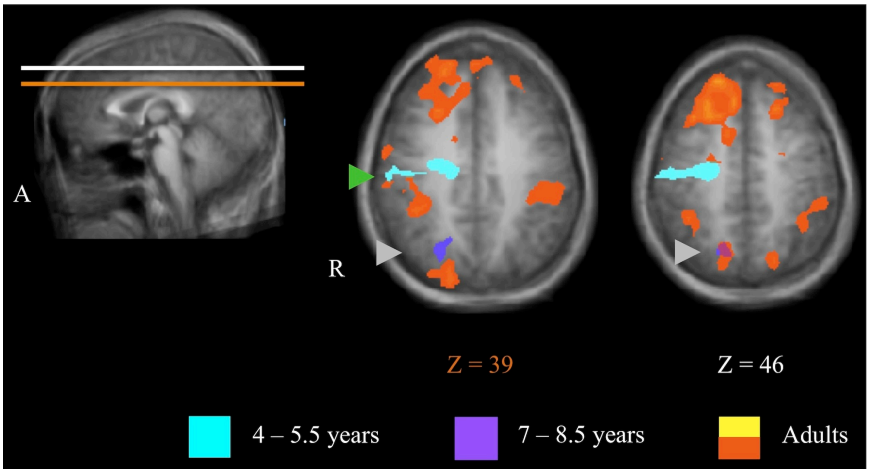

Figure 8. Haptic object preference (HO > HT). Group maps are presented at a threshold of $p < 0.05$ (corrected). Overlapping activations are located in dorsal regions: the right caudal IPS (gray arrow), and the right postcentral gyrus (green arrow).

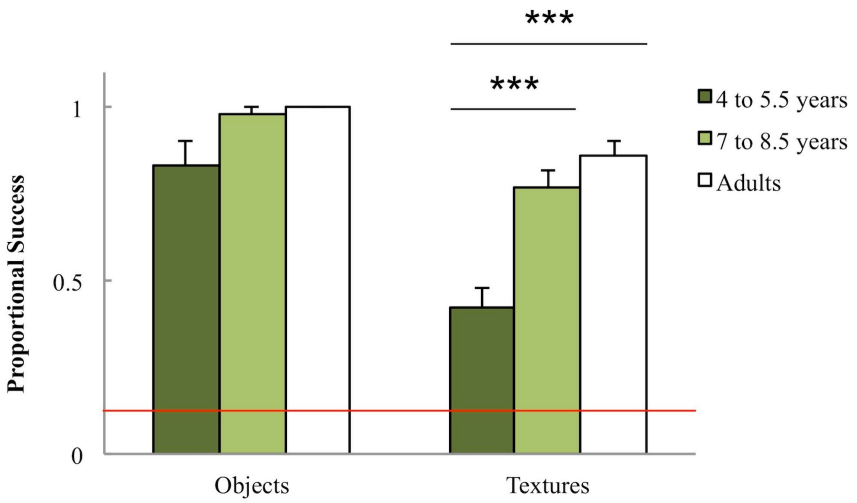

Figure 9. Proportional success of the behavioral match-to-sample task. Objects and textures are compared across age during crossmodal haptic-to-visual recognition. Red line indicates chance performance.

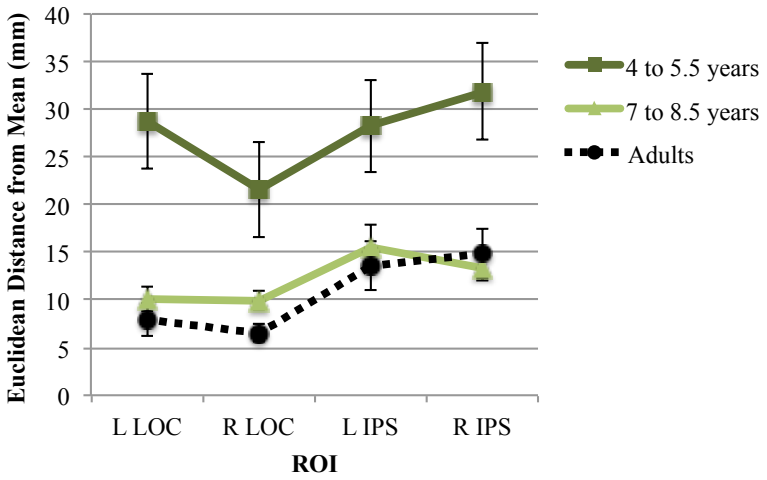

Figure 10. Variability of individual ROI locations as a function of age group. Mean Euclidean distance from the prototypical ROI center is shown for each ROI for each age group. Error bars represent SEM.

Supplementary material

Motion tolerance threshold analyses

Analyses were performed to examine the differences in motion between age groups, as well as the impact of motion artifacts on the BOLD signal when using a tolerance threshold of 5 mm. Mean motion was used as the primary measure of in-scanner head movements in these supplemental analyses, and was calculated from the translation and rotation parameters across the three axes. This standard measure of mean displacement has been shown to be an adequate metric for assessing head motion both in adults and in children (Satterthwaite et al., 2012; Van Dijk, Sabuncu, & Buckner, 2012).

Results indicated that young children aged 4 to 5.5 years did indeed produce more head movements than older children aged 7 to 8.5 years ($t(26) = 1.83$, $p < .05$), and adults ($t(21) = 2.52$, $p < .01$). The mean motion (mm) of each age group is shown in Fig. S1; the mean head displacement of individual participants from each age group is shown in Fig. S2. Additionally, although adult head motion, even measured by using maximum head displacement (mm), was consistently below 1 mm, the total number of useable participants would have decreased drastically as the threshold became stricter (Table S1). From these data, is it clear that the use of a more liberal threshold allows for more children to be retained in the data set, while a stricter criterion would be highly impractical.

Nevertheless, it is possible that the tendency for the young children to move their heads more than the older children or adults could have driven the differences in BOLD activation. To allay this concern, BOLD signal change for visual object preference in the

LOC—the dependent measure that produced the largest effect—was compared to mean motion. In each age group, the correlation between the two measures was not significant (4 to 5.5 year olds: ($r^2(13) = .21$, $p = n.s.$); 7 to 8.5 year olds: ($r^2(11) = .05$, $p = n.s.$); adults: ($r^2(6) = .03$, $p = n.s.$)).

Taken together with the similar developmental patterns of individual ROI variability, these analyses suggest that 4-to 5.5-year-old children are clearly dissimilar from 7- to 8.5-year-old children and adults. This is different from the primary ROI findings for vision in which there was a separation between the two groups of children and the adults. As such, it is unlikely that the differences in neural activity can be accounted for by head movements.

Individually-defined ROI analysis

For comparison with the group-defined ROI analysis, an individually-defined ROI analysis was performed. A 2 x 2 x 3 repeated measures ANOVA was used with stimulus type (objects and textures) and sensory modality (vision and haptics) as the within-subjects factors, age group (4 to 5.5 year olds, 7 to 8.5 year olds, and adults) as the between-subjects factor, and BOLD signal change (beta weights) as the dependent variable in the LOC and in the IPS. For consistency, the data for each region were collapsed across hemisphere. It is important to note that three participants from the 4 to 5.5 year old age group were discarded from each bilateral region due to difficulties in localizing the appropriate regions.

The BOLD signal change responses for the two bilateral ROIs in the complete design are shown in Fig. S3A-B. In the LOC, results indicated a main effect of age group

($F(2,30) = 8.42$, $p < .001$, $MSe = 1.83$), and of stimulus type ($F(1,30) = 74.67$, $p < .001$, $MSe = 4.25$) with a greater response for objects than textures overall ($t(32) = 7.42$, $p < .001$), as well as within each group (4 to 5.5 year olds: ($t(11) = 3.12$, $p < .01$); 7 to 8.5 year olds: ($t(12) = 4.56$, $p < .001$); adults ($t(7) = 8.55$, $p < .001$)). There was no main effect of modality. There was, however, a significant interaction of stimulus type by age group ($F(2,30) = 4.63$, $p < .05$, $MSe = .26$); this is shown in Fig. S4A. As revealed by post-hoc *t*-tests, BOLD activation increased with objects across age—responses were significantly greater in the adults than in the 4- to 5.5-year-old children ($t(18) = 3.87$, $p < .01$), and in the 7 to 8.5 year olds ($t(19) = 3.41$, $p < .01$). In the IPS, results showed a main effect of stimulus type ($F(1,30) = 37.62$, $p < .001$, $MSe = 2.26$) with a bias for objects over textures (overall: ($t(32) = 5.14$, $p < .001$); 4 to 5.5 year olds: ($t(11) = 4.72$, $p < .001$); 7 to 8.5 year olds: ($t(12) = 6.88$, $p < .001$); adults ($t(7) = 6.46$, $p < .001$)). Similar to the findings in bilateral LOC, there was a significant stimulus type by age group interaction (($F(2,30) = 4.36$, $p < .05$, $MSe = .26$); Fig. S4B), with post-hoc *t*-tests revealing a trend toward increasing activation with objects between the 4 to 5.5 year olds and the adults ($t(21) = 1.93$, $p = .069$). Additional key results included differences in activation for visual objects between adults and 4- to 5.5-year-old children (LOC: ($t(18) = 5.07$, $p < .001$); IPS: ($t(18) = 2.21$, $p < .05$)), and between adults and 7- to 8.5-year-old children (LOC: ($t(19) = 3.90$, $p < .001$); IPS: ($t(19) = 2.16$, $p < .05$); Fig. S3A-B).

Object preference—the difference in BOLD activation between objects and textures for both vision and haptics (i.e., VO > VT; HO > HT)—was also examined in the LOC and IPS (Fig. S5). In the LOC, significant biases for visual over haptic object preference were found in all three age groups (4 to 5.5 year olds: ($t(11) = 2.87$, $p < .05$); 7

to 8.5 year olds: ($t(12) = 2.48$, $p < .05$); adults ($t(7) = 3.28$, $p < .05$); Fig. S5A). Furthermore, adults showed greater visual preference than the 7- to 8.5-year-old children ($t(19) = 2.42$, $p < .05$), and the 4- to 5.5-year-old children ($t(21) = 3.57$, $p < .01$). In bilateral IPS, visual object preference followed a similar pattern wherein adults showed significantly greater activation than the 7- to 8.5-year-old children ($t(19) = 2.14$, $p < .05$), with a trend toward higher preference in adults than the 4- to 5.5-year-old children (($t(18) = 1.76$, $p = .096$); Fig. S5B). Haptic preference was not reliably different among the three groups in either of the bilateral ROIs.

Overall, there were slight differences between the individually- and group-defined ROIs. The results from the selection of individual-based ROIs showed a bias for visual over haptic object preference in the LOC for all age groups—a finding that was not apparent in the group-based ROIs. Moreover, the 4- to 5.5-year-old children, who demonstrated the greatest variability in terms of ROI location as well as head motion, showed a stronger BOLD response relative to baseline for object preference in the individually-defined ROIs than in the group-defined ROIs. Given the higher variability in only one of the three age groups, it is possible that the individual ROI analysis could have yielded different results. This is especially so when considering the difficulty in localizing all of the regions in young children individually. Even with the loss of a few participants, however, all three age groups showed some increases in percentage BOLD signal change, thus producing results with very similar patterns as the group analysis measuring activity from the same neural substrates across all participants.

Therefore, while there were some additional effects, the results of the individual ROI analysis confirmed the primary findings from the group-defined ROIs. Specifically,

both analyses indicated a developmental increase in visual object preference in the LOC that was not yet adult-like by 8.5 years of age. The dissociation between the developmental trajectories of vision and haptics—where adult-like haptic object preference is reached earlier than visual object preference—in the LOC was also supported by evidence from the individual-based ROI analysis. Finally, the pattern of responses in the IPS was similar to the LOC in which adults showed a visual dominance in object preference as compared to children, whereas haptic object preference was constant between 4 years and adulthood.

Supplementary references

Satterthwaite, T. D., Wolf, D. H., Loughead, J., Ruparel, K., Elliott, M. A., Hakonarson, H., Gur, R. C., & Gur, R. E. (2012). Impact of in-scanner head motion on multiple measures of functional connectivity: Relevance for studies of neurodevelopment in youth. *NeuroImage, 60*, 623-632.

Van Dijk, K. R. A., Sabuncu, M. R., & Buckner, R. L. (2012). The influence of head motion on intrinsic functional connectivity MRI. *NeuroImage, 59*, 431-438.

Table S1. Number of participants included at different motion tolerance thresholds.

Motion Threshold	Total No.	4 to 5.5 years	7 to 8.5 years	Adults
5 mm	36	15	13	8
4 mm	31	12	11	8
3 mm	26	9	9	8
2 mm	20	6	6	8
1 mm	11	2	1	8

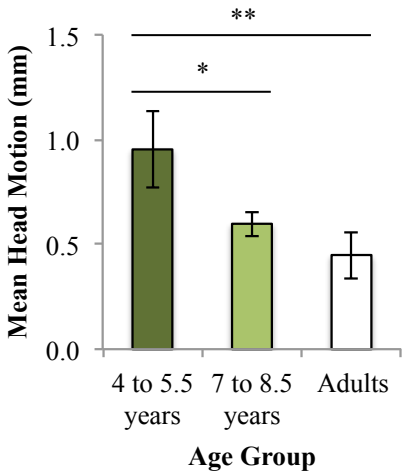

Figure S1. Mean head motion (in mm) for each age group. On this and subsequent figures, * denotes $p < .05$, ** denotes $p < .01$, *** denotes $p < .001$. Error bars represent SEM.

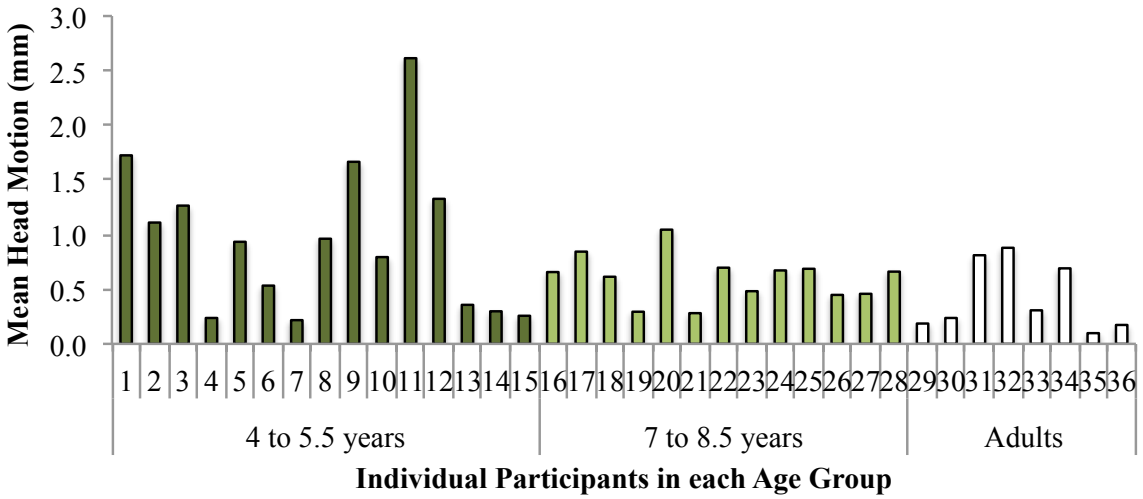

Figure S2. Mean head motion (in mm) for each individual participant within each age group.

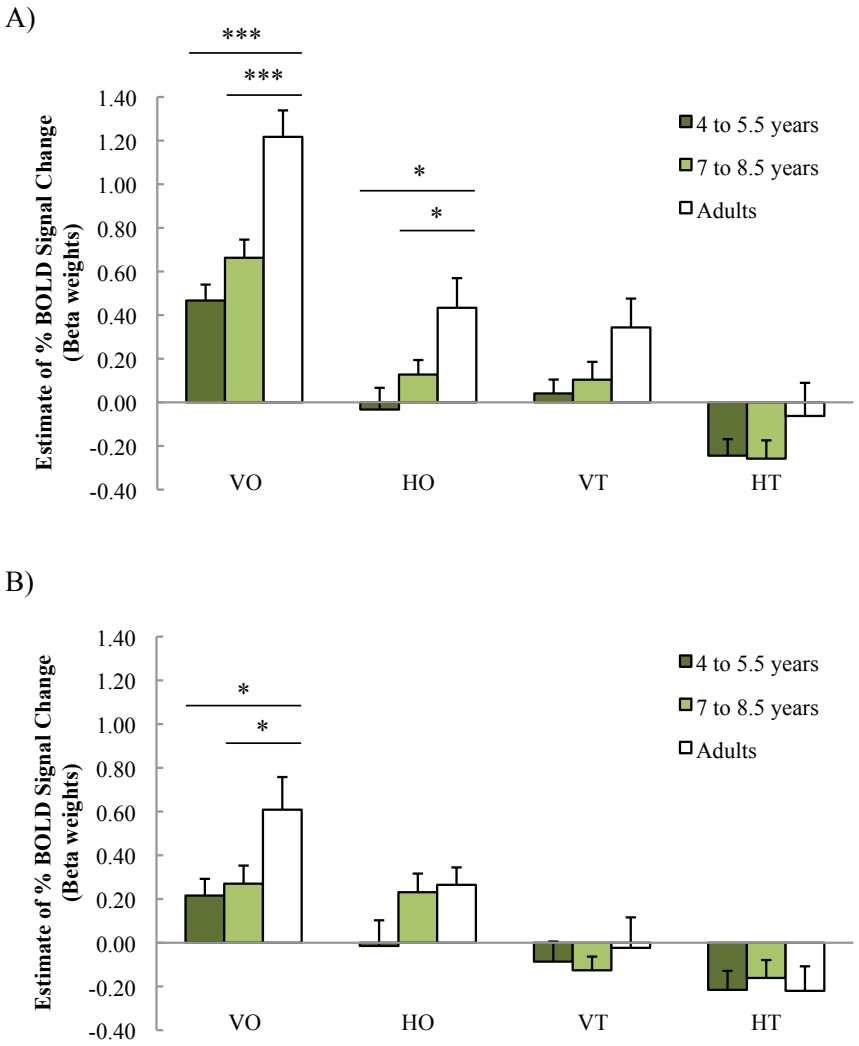

Figure S3. BOLD signal change of the complete design in bilateral LOC (A) and IPS (B).

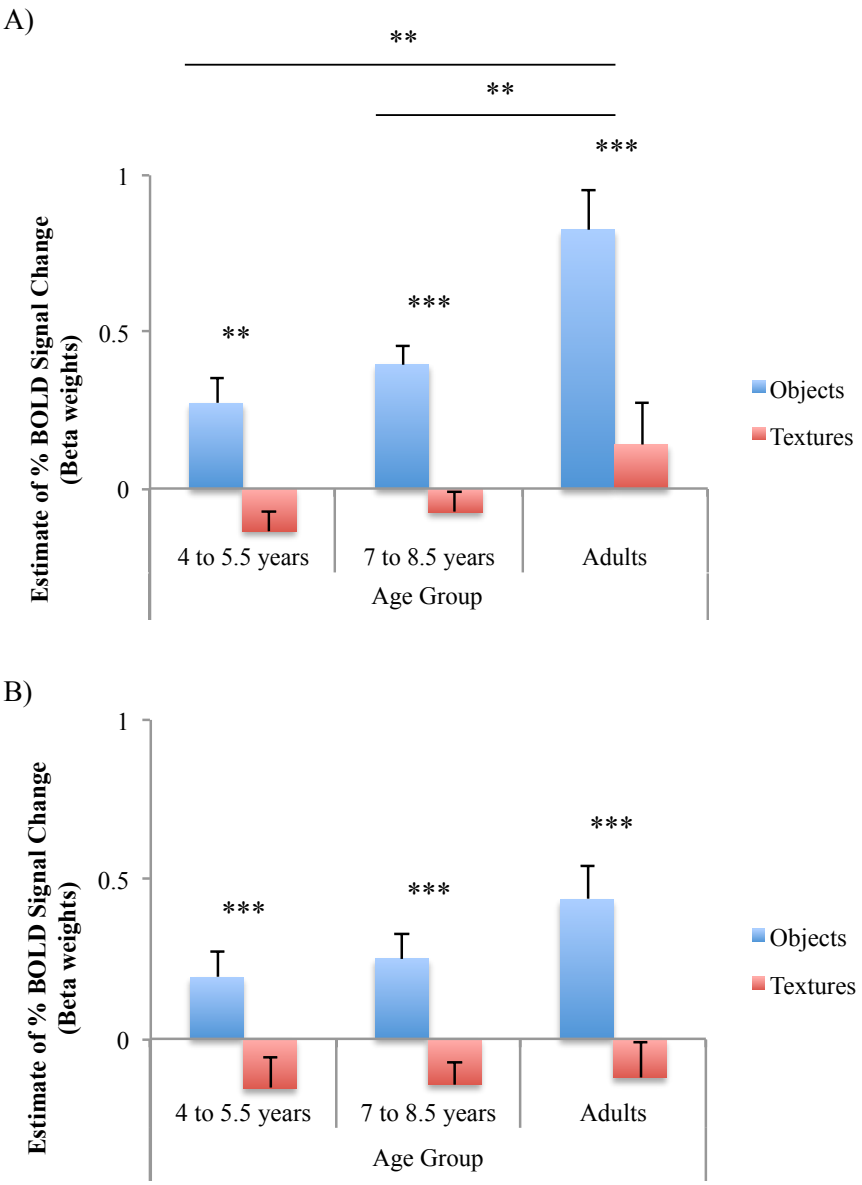

Figure S4. Objects compared to textures by age. BOLD signal change is shown as a function of age group and stimulus type collapsed across modality (i.e., VH objects, VH textures) in bilateral LOC (A) and IPS (B).

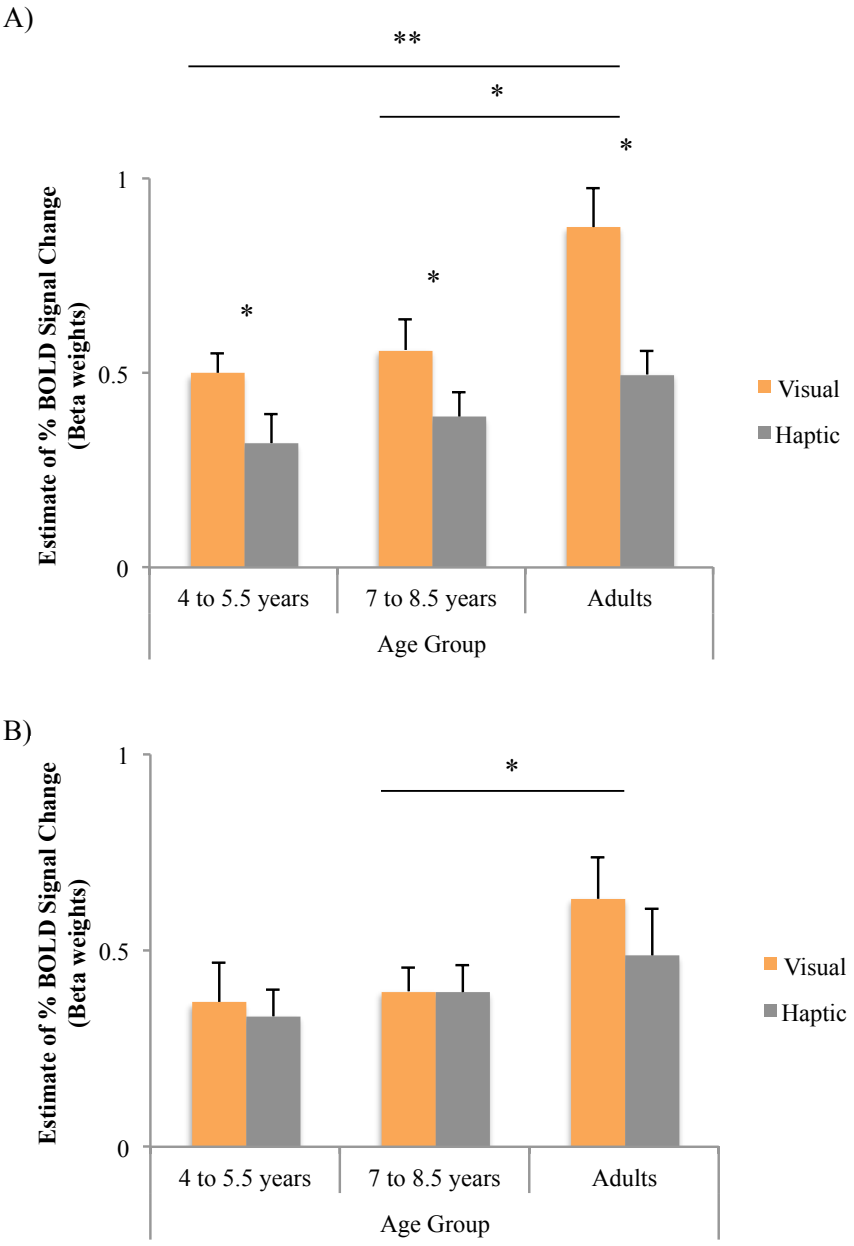

Figure S5. Visual object preference compared to haptic object preference by age. BOLD signal change is shown as a function of age group and object preference (i.e., objects > textures) by modality in bilateral LOC (A) and IPS (B).

Chapter 3.

Crossmodal Enhancement in the LOC for Visuohaptic Object Recognition Over Development

Abstract

Research has provided strong evidence of multisensory integration of visual and haptic information within the visual cortex. These studies implement crossmodal matching paradigms to examine how systems use information from different sensory modalities for object recognition. Developmentally, behavioral evidence of visuohaptic crossmodal processing has suggested that communication within sensory systems develops earlier than across systems; nonetheless, it is unknown how the neural mechanisms driving these behavioral effects develop. To address this gap in knowledge, BOLD functional Magnetic Resonance Imaging (fMRI) was measured during delayed match-to-sample tasks that examined intramodal (visual-to-visual, haptic-to-haptic) and crossmodal (visual-to-haptic, haptic-to-visual) novel object recognition in children aged 7 to 8.5 years and adults. Tasks were further divided into sample encoding and test matching phases to dissociate the relative contributions of each. Results of crossmodal and intramodal object recognition revealed the network of known visuohaptic multisensory substrates, including the lateral occipital complex (LOC) and the intraparietal sulcus (IPS). Critically, both adults and children showed crossmodal enhancement within the LOC, suggesting a sensitivity to changes in sensory modality during recognition. These groups showed similar regions of activation, although children generally exhibited more widespread activity during sample encoding and weaker BOLD signal change during test

matching than adults. Results further provided novel evidence of a bilateral region in the occipitotemporal cortex that was haptic-preferring in both age groups. This region abutted the bimodal LOtv, and was consistent with a medial to lateral transition from a visual to haptic bias within the LOC. These findings converge with existing evidence of visuohaptic processing in the LOC in adults, and extend our knowledge of crossmodal processing in adults and children.

3.1. Introduction

Vision is the dominant perceptual modality in humans. This is especially true for object recognition – a ubiquitous and highly important cognitive function – and particularly for recognizing objects based on their three-dimensional shape. However, it has been demonstrated that, in the absence of vision, accurate recognition of objects based on shape cues can be accomplished using haptic input alone (Klatzky, Lederman, & Reed, 1987; Lederman & Klatzky, 1987, 1990, 1993; Norman et al., 2004, 2008). In addition to these unisensory findings, there is evidence that visual and haptic inputs are effectively combined to enhance recognition performance (Kim & James, 2010; Kim, Stevenson, & James, 2012), and that the haptic modality can successfully prime the visual modality and vice versa (Easton, Greene, & Srinivas, 1997; James et al., 2002). Finally, it has been shown that objects can be successfully matched when studied either visually or haptically, and then tested with the other modality (i.e., crossmodal matching; James, Kim, & Fisher, 2007; Kassuba et al., 2013; Newell et al., 2001). Combined, this evidence suggests that the visual and haptic systems are tuned to the shape properties of objects, and furthermore, that they share shape information and perhaps even common

representations for the purposes of object recognition (Amedi et al., 2005; James et al., 2005; Lacey & Sathian, 2011).

For the past two decades, a body of evidence has been accrued suggesting that regions of the putative visual and haptic cortices are involved in combining visual and haptic information about object shape. This research has increasingly concentrated on multisensory object recognition, and more specifically, on visuohaptic integration (Amedi et al., 2001, 2002; James et al., 2002; James & Kim, 2010; Kassuba et al., 2013; Lacey & Sathian, 2011; Lacey et al., 2009; Gentile, Petkova, & Ehrsson, 2011; Stilla & Sathian, 2008). Several neuroimaging studies have determined that this convergence of visuohaptic information in adults occurs most commonly at two particular brain regions: the lateral occipital complex (LOC; Amedi et al., 2001, 2002; James et al., 2002; Stoesz et al., 2003; Reed et al., 2004; Prather, Votaw, & Sathian, 2004; Pietrini et al., 2004), and the intraparietal sulcus (IPS; James & Kim, 2010; Bodegard et al., 2001; Binkofski et al., 1999; Culham & Kanwisher, 2001; Grefkes et al., 2002; Peltier et al., 2007; Roland et al., 1998; Zhang et al., 2004; Stilla & Sathian, 2008). The LOC is a large collection of regions, including the anterior aspects of the inferior and middle occipital gyri, the posterior aspects of the middle and inferior temporal gyri, and a large section of the occipital and temporal fusiform gyrus. The LOC has been found to respond more to (images of, and three-dimensional forms of) visual presentations of intact objects such as tools, animals, toys, etc., as compared to scrambled versions of the same objects or textures (Amedi et al., 2001; Grill-Spector, Kourtzi, & Kanwisher, 2001; Grill-Spector, Golarai, & Gabrieli, 2008; James & Kim, 2010; Kassuba et al., 2011; Kourtzi & Kanwisher, 2001; Malach et al., 1995; Tootell et al., 1996). In addition, the lateral

occipital tactile-visual region (LOtv) contained within the complex, activates during haptic presentations of those objects compared to textures (Amedi et al., 2001, 2002; James et al., 2002; Stilla & Sathian, 2008).

The IPS is a one of the primary landmarks of the parietal lobe and runs from the occipitoparietal junction to cross the postcentral sulcus. The anterior aspect of the IPS (aIPS) lies near the postcentral gyrus and has been commonly reported to activate during haptic shape perception (Bodegard et al., 2001; Culham & Kanwisher, 2001; Peltier et al., 2007; Roland et al., 1998; Stilla & Sathian, 2008; Zhang et al., 2004). Furthermore, the anterior and posterior aspects of the IPS have been shown to activate during the crossmodal matching of two- and three-dimensional objects (Grefkes et al., 2002; Saito et al., 2003), demonstrating a preferential response for overall object shape regardless of sensory modality. The object-responsive IPS has been found to activate not only to common, familiar objects (Amedi et al., 2001, 2002, 2005; Deibert et al., 1999; Reed et al., 2004), but to simple, geometrical shapes as well (Bodegard et al., 2001; Roland et al., 1998). Similarly, the LOC has been found to respond to both familiar and novel shape information (Lacey, Flueckiger, Stilla et al., 2010; Lacey, Stilla, Sreenivasan et al., 2014). Taken together, this accrual of evidence implicates the LOC and IPS as sites of convergence in which visuohaptic information is processed for the analysis of object shape.

Relative to adult research, there are far fewer neuroimaging studies that have investigated the development of crossmodal perception of visual and haptic information. Yet, a full understanding of the mechanisms of visuohaptic convergence requires an understanding of their development. In fact, understanding how convergence of sensory

systems develops may provide unexpected insights into the mechanisms of adult multisensory processing. Behavioral studies that have researched this question suggest that communication within sensory systems generally develops earlier than communication across sensory systems (Bushnell & Baxt, 1999). Additionally, research has shown that the manner in which infants and children haptically explore objects influences concurrent and later visual perception (Ruff, 1984, 1986, 1989; Bushnell & Boudreau, 1993), and more adult-like patterns of visuomotor exploration at 24 months result in an increase in some measures of visual object recognition (James, Swain, Jones, & Smith, 2013). By 4 to 5 years of age, children's patterns of haptic object exploration begin to appear stereotypically adult-like (Kalagher & Jones, 2011a, 2011b), and intramodal haptic object recognition is highly accurate (Bushnell & Baxt, 1999). Nevertheless, crossmodal visuohaptic recognition abilities at this age are not yet adult-like. At 5 years, children demonstrate poorer crossmodal performance compared to intramodal visual-to-visual or haptic-to-haptic recognition for novel objects (Bushnell & Baxt, 1999). It is not until 8 to 10 years that the integration of visual and haptic shape information becomes statistically optimal according to psychophysical discrimination tasks, which suggests a developmental transition prior to this age range (Gori et al., 2008). As such, the behavioral delay in crossmodal processing is thought to be due to the lack of efficiency in integrating or transferring information from one modality to another before 8 years of age.

More is known about the neural mechanisms that underlie the developmental progression of visual than of haptic object recognition. For vision, there is evidence that the LOC is generally recruited during visual object perception by 7 years (Grill-Spector,

Golarai, & Gabrieli, 2008; Scherf et al., 2007). This recruitment may be experience-dependent as evidenced by differential LOC recruitment among similarly aged children based on the level of experience with select object classes (James & James, 2013). Thus, although the LOC is recruited for visual object recognition early on in development (i.e., by 7 years of age), the specific pattern of recruitment of the LOC and of the surrounding cortex continues to develop after 7 years (Grill-Spector, Golarai, & Gabrieli, 2008; Scherf et al., 2007). In a previous study by our lab, we found that unisensory haptic object preference was adult-like by 4 to 5.5 years, whereas visual object preference continued to increase into young adulthood at which point it was quite visually dominant (Jao, James, & James, 2014). A key conclusion of these findings was that the apparent level of maturation of function within a particular neural substrate is task-dependent.

As such, the goal here was to examine visuohaptic interactions with respect to crossmodal matching. We implemented a delayed match-to-sample paradigm and measured blood oxygen level dependent (BOLD) responses in 7- to 8.5-year-old children and young adults during crossmodal visuohaptic and intramodal visual and haptic processing of novel objects. Novel objects were used, based on previous findings of behavioral differences during crossmodal and intramodal tasks for unfamiliar objects (Bushnell & Baxt, 1999). The age groups were chosen to encompass the estimated age interval of the developmental transition for visuohaptic integration as indicated by previous behavioral and neural reports (Gori et al., 2008; Grill-Spector, Golarai, & Gabrieli, 2008; Jao, James, & James, 2014; Scherf et al., 2007). Given this previous work, we predicted a stronger response for crossmodal than intramodal matching in adults, and possibly in children (i.e., the crossmodal matching effect in IPS; see Grefkes

et al., 2002). Moreover, we predicted that the marker used to indicate efficient crossmodal sharing of sensory information, namely crossmodal enhancement (Kim & James, 2010; Kim, Stevenson, & James, 2012), would be less pronounced in children, reflecting their decreased ability to integrate visual and haptic information about object shape.

3.2. Methods

3.2.1. Participants

Participants were recruited from two age groups: 7 to 8.5-year-old children (N = 11, 5 female, mean age = 7.8 years, σ = 0.4 years) and young adults (N = 10, 5 female, mean age = 25.8 years, σ = 5.7 years). Three additional children were tested, but were excluded from analyses due to excessive motion (2) and high variability (1). Participants had normal or corrected to normal vision, had no known history of psychological disorders, and were predominantly right-handed (7 to 8.5 years: 1 ambidextrous, 1 slight left-preferring, 9 right-preferring; Adults: 10 right-preferring) as measured by the Edinburgh Handedness Inventory (Oldfield, 1971; for a discussion of handedness, see subsection *3.4.4. Handedness and the LOC*). All met the criteria for MRI scanning. Written informed consent was obtained from the parents and adult participants, and written informed assent was obtained from the children. Parents were compensated with a gift certificate, children were compensated with a small toy, and adult participants were compensated with $25. This research was approved by the Indiana University Protection of Human Participants Board.

3.2.2. Stimuli

The stimuli consisted of 20 objects that were explored visually and haptically. Stimuli

were novel, three-dimensional, and had rigid bodies that were controlled for texture (i.e., all objects were printed in plastic using a 3-D printer) (Fig. 1). The visual stimuli consisted of gray scale photographs of the haptic stimuli at a typical three-quarters viewing angle against a solid black background to facilitate recognition during visual exploration. Stimuli were further controlled for size to ensure that the younger group of participants could fit both of their hands around them during haptic exploration; objects were no greater than 9 cm along the longest dimension, and no smaller than 2.5 cm along the shortest dimension. Participants did not see or feel the objects prior to the training session that occurred before the imaging session.

3.2.3. Procedure

After screening and obtaining informed consent from the adults and assents from the children, all participants were acclimated to an MRI environment. Children watched as a short cartoon was played on a screen in the MRI simulator, an artificial MRI environment with the same dimensions and sounds as the actual MRI environment. Participants were then trained in the experiment. They were instructed to lie very still in a supine position, and a lap desk was placed over their midsection. A cape was placed over their torso and arms, and was tucked under their chin. This cape covered the lap desk and allowed the participants to feel the stimuli with their hands without being able to see them. Participants were trained to perform four types of delayed match to sample tasks following the instructions: 1) "Look;" 2) "Feel;" 3) "Look, then feel;" and 4) "Feel, then look." The delayed match to sample tasks were further separated into two phases: 1) the sample encoding phase; and 2) the test matching recognition phase. The first two types of instructions yielded intramodal matching (i.e., visual-to-visual or "VV," haptic-to-haptic

or “HH”) in which the same modality was used to encode and recognize the stimuli. The latter two types of instructions resulted in crossmodal matching (i.e., visual-to-haptic or “VH,” haptic-to-visual or “HV”) in which one modality was used to encode the stimulus and another modality for testing recognition as well as crossmodal sharing of object shape information. During the encoding phase for each type of delayed match to sample task, participants were instructed to look at or feel the sample stimulus. They were then tested on intramodal and crossmodal recognition with three objects sequentially, each of which they had to decide if it was the same as or different from the sample stimulus. Participants verbally indicated their responses during the training tasks, and were able to do so correctly with ceiling levels of performance (i.e., participants in each group for each task responded correctly on all trials).

Once the participants were comfortable in this setting and could perform the tasks efficiently, they were introduced to the actual MRI environment. It was decided based on several reasons that behavioral responses would not be recorded during the MRI scan. First, the preferred mode for haptic exploration of 3D objects is with two hands for adults and children. To include a button press response would restrict exploration to the unnatural single-handed mode, which would likely be more distracting for children than adults. Alternatively, exploration could be two-handed, followed by a button press, but finding the location of the button without being able to visually locate it would be challenging, as would returning to the start position for haptic exploration. This alternative would likely be more challenging for children than adults. Outside the MRI environment, verbal responses would be an excellent candidate to combine with two-handed exploration, but collecting verbal responses within the MRI scanner introduces

considerable artifacts into the BOLD signal. Another possibility would be foot-button presses as responses; however, this type of response produces significantly more head motion in adult participants (Kim & James, 2010; unpublished data) and was dismissed as an option because of the likelihood of extreme head movements it may have produced in children. Finally, these considerations were in addition to the fact that the delayed match-to-sample task is already relatively cognitively challenging, especially when considering the working memory load involved with keeping one of four instructional contexts in mind while performing that task. The final choice to eliminate behavioral responses from the MR experimental protocol was based on our previous developmental neuroimaging findings showing that forcing children to perform tasks that are too cognitively or attentionally demanding results in early withdrawal or, when they do not withdraw, increased head and body motion. Instead of measuring behavior during the MR protocol, performance was measured beforehand during training to ensure that they could perform as well as adults, which was indeed the case. In terms of ensuring an equal level of task compliance between adults and children, an experimenter was present in the MR room during the experiment to monitor the participant's behavior, including task compliance and body and head movement.

Once in the MRI, participants were again given the instructions, and the lap desk and cape were placed over their midsection. All visual stimuli were back-displayed via a Mitsubishi XL30 projector onto a screen located behind the participants in the bore of the MRI; this screen was viewed through a mirror that was placed on top of the head coil. Visual stimuli were presented using SuperLab Pro 2.0.4 software from an Apple MacBook laptop. Haptic stimuli were exchanged by an experimenter who stood next to

the MRI, and were attached to the lap desk with Velcro so that participants could not lift the objects off of the surface during exploration. Participants viewed the visual stimuli with both eyes, and explored the haptic stimuli using both hands.

A high-resolution anatomical scan was first acquired, which for children, occurred as they watched a cartoon. Upon completion of this scan, four functional scans were acquired. Participants were tested using a mixed event-related/block design that involved intramodal visual encoding and recognition of 2D images of the stimuli, intramodal haptic encoding and recognition of the 3D stimuli, as well as crossmodal visual-to-haptic and haptic-to-visual encoding and recognition of the stimuli. Examples of all 4 tasks are depicted in Fig. 2. For each type of task, instructions were presented for 4 s, followed by a 2 s inter-stimulus-interval (ISI). The sample stimulus was then presented for 4 s. After a variable delay of 4 or 6 s in between sample and test, the test stimuli were presented sequentially for 2 s with a 2 s ISI between each. An inter-trial-interval (ITI) of 2 s, during which participants viewed a gray fixation cross, separated trial sets—a set comprised the instructions, sample presentation, delay, and test presentations. Finally, an inter-block-interval (IBI) of 10 s was presented at the beginning and end of each run. It is important to note that in order to dissociate the relative contributions of sample and test during intramodal and crossmodal matching, trial sets were not evaluated as a compound event (for a brief critique, see Kassuba et al., 2013). Rather, the variable delay allowed for later deconvolution of the neural signal into the two phases.

Throughout the functional scanning session, participants viewed a black background on which the visual instructions, visual stimuli, and gray fixation cross (ISI, ITI, IBI) were presented, or a blank screen was displayed. Since instructions were given

visually, participants were instructed to keep their eyes open during haptic exploration; therefore, the screen remained blank during and between presentations of haptic stimuli.

The experiment consisted of 32 event-related sample trials (8 per task) and 96 blocked test trials (24 per task) in total, separated into 4 runs of approximately 4-minute-long functional scanning (230 s, 115 volumes) with 8 trial sets per run. Trials were pseudo-randomized such that each trial set consisted of at least one match and one mismatch between the test and sample stimuli. Each run comprised of either VV and VH conditions (visual encoding tasks) or HH and HV conditions (haptic encoding tasks). This was to ensure that the modality used during the encoding phase was consistent across the run, and to minimize task-switching errors, particularly by the children. Tasks were counterbalanced across runs, and run order was randomized for each participant. Imaging sessions lasted approximately 30 minutes. After the scanning was completed, participants were removed from the MRI environment and compensated for their time.

3.2.4. MRI data acquisition

Imaging was performed using a 3-Tesla Siemens Magnetom Trio whole body MRI system located within the Imaging Research Facility at the Indiana University Psychological and Brain Sciences department. A phased array 12 channel head coil was used to obtain whole-brain functional volumes; these were acquired using a gradient echo planar imaging (EPI) sequence (TE = 30 ms, TR = 2000 ms, flip angle = 70°) for BOLD-based imaging. The field of view was 192 cm with an in-plane resolution of 64 x 64 pixels and 33 slices per volume (3.8 mm thick with a 0 mm gap), which resulted in a voxel size of 3 x 3 x 3.8 mm. Using analysis tools in the BrainVoyager QX^{TM} 2.4 software package (Brain Innovation, Maastricht, Netherlands), functional data underwent

slice scan-time correction, 3D motion correction, linear trend removal, and Gaussian spatial blurring (FWHM 6 mm). High-resolution T1-weighted anatomical volumes (resolution: 1.5 x 1.5 x 1.5 mm, 120 sagittal slices) were acquired prior to the functional imaging using a 3-D Turbo-flash inversion recovery sequence. Individual functional volumes were co-registered to the anatomical volumes with an intensity-matching, rigid-body transformation algorithm. Anatomical and functional volumes were normalized to a standard space using an affine transformation based on the 8 parameters of the Talairach reference (Talairach & Tournoux, 1988). For a discussion of the concerns regarding comparisons between children and adult brains normalized to a standard, stereotactic atlas such as the Talairach space, see Appendix B of Wakefield, James, and James (2013). During normalization, voxels of the functional volumes were resampled to 3 mm^3.

3.2.5. Data analysis procedures

3.2.5.1. Group contrasts

Whole-brain statistical parametric maps (SPMs) were calculated using the BrainVoyager QX™ 2.4 analysis package. Data were transformed into a common stereotactic space (e.g., Talairach & Tournoux, 1988) for group-based statistical analyses. Functional data were analyzed using a random effects general linear model (GLM) with group as a between-subjects factor. Two predictors were entered in the design matrix for each of the four crossmodal or intramodal conditions. The onset time of the first predictor was based on the sample stimulus presentation time (sample encoding phase) and the onset time of the second predictor was based on the onset of the block of test stimuli (test matching phase). These predictors were convolved with a two-gamma hemodynamic response

function. Motion parameters were also included in the design matrix as predictors of no interest. Functional runs with motion estimates exceeding 5 mm on any axis were excluded from the analyses. Although this is a more liberal threshold than is often used in studies with only adults, it was adopted as the criterion here because a stricter criterion would have eliminated most of the child participants (see subsection 3.2.5.3. Motion tolerance threshold analyses). This criterion resulted in a total of 42 runs (on average, 3.8 runs per participant) for the children, and 40 runs (4 runs per participant) for the adults.

The whole-brain contrasts were thresholded using a minimum voxel-wise *p*-value of < .001 per map, and corrected for multiple tests using a cluster threshold of at least 29 voxels as determined by Monte Carlo simulation using the BrainVoyager QX™ Cluster-size Estimation Plug-in. This plug-in estimates the cluster-size threshold required to produce an alpha < .05 based on a specific voxel-wise *p*-value.

3.2.5.2 Post-hoc Region-of-Interest selection

A post-hoc Region-of-Interest (ROI) analysis was performed on a group-defined ROI in the LOC to examine the effects of crossmodal and intramodal processing during the test matching phase. To localize this ROI, four whole-brain SPMs were calculated during the sample encoding phase using random-effects GLMs and balanced contrasts. These contrasts compared: a) adult vision to rest (VV + VH > 2 x rest); b) adults haptics to rest (HH + HV > 2 x rest); c) 7 to 8.5 year old vision to rest (VV + VH > 2 x rest); and d) 7 to 8.5 year old haptics to rest (HH + HV > 2 x rest). The LOC was selected as the overlap between all four contrasts in the left hemisphere. Previous studies have demonstrated robust effects in the left hemisphere (Kim & James, 2010; Kim, Stevenson, & James, 2012), and while our results showed no difference between hemispheres, we primarily

show the data from the left hemisphere for convenience. This region was comparable in terms of anatomical overlap to the LOtv area indicated by a previous study that compared visuohaptic object-selectivity directly (i.e., (VO > VT) ∩ (HO > HT); Jao, James, & James, 2014). Thus, given the location of this ROI, it appears to reflect a similar functional region of cortex (i.e., LOtv) as indicated by other studies (e.g., Amedi et al., 2001, 2002; Amedi, Raz, Azulay, et al., 2010; Kim, Stevenson, & James, 2012), and provides an adequate proxy for LOC ROIs defined using a more standardized task.

A secondary post-hoc ROI analysis was conducted on group-defined ROIs located medially and laterally to the left LOC ROI. These regions were localized using overlapping difference maps comparing vision to haptics (VV + VH > HH + HV) in each group during the sample encoding phase. The medial (fusiform gyrus) and lateral (middle temporal/occipital gyrus) ROIs were examined for differential effects of modality, as well as of crossmodal vs. intramodal processing, in relation to the overlap (LOC) ROI during the test matching phase.

BOLD time courses were extracted from these ROIs during the test matching phase for each condition using event-related averaging. BOLD activation values were calculated for each participant for each condition as the mean BOLD signal change that was time locked to the onset time of the block of test stimuli (i.e., between 14 to 16 s post-trial onset, which began with the instructions) to measure activation during the test matching phase. Two dependent measures were of interest, including: a) the test trial type–this measure was based on crossmodal (VH and HV) versus intramodal (VV and HH) matching; and b) the test modality–this measure was based on the sensory modality used to match the test stimulus to the sample stimulus (vision: VV and HV; haptics: HH

and VH). For the LOC ROI, BOLD activation values were used as the dependent measure in a 2x2x2 split-plot repeated measures analysis of variance (ANOVA) performed in SPSS with group as a between-subjects factor and modality and trial type as within-subjects factors. For the medial, overlap, and lateral ROIs, BOLD activation values were used as dependent measures in a 2x2x2x3 split-plot repeated measures ANOVA with group as a between-subjects factor and modality, trial type, and ROI as within-subjects factors.

3.2.5.3 Motion tolerance threshold analyses

Motion tolerance threshold analyses were conducted to examine age-related differences in motion, and the impact of motion artifacts on the BOLD signal (see supplementary materials in Jao, James, and James (2014) for a detailed description).

Results showed that children aged 7 to 8.5 years did produce greater head motion than adults ($t(19) = 4.280$, $p < .001$). The mean motion (mm) for each age group is presented in Fig. 3; the mean head displacement (mm) of individual subjects is presented in Fig. 4. Although adult head motion, measured using mean motion (mm) or maximum head displacement (mm), was predominantly below 1 mm, the number of retainable subjects in the group of 7 to 8.5 year olds would have decreased substantially as the threshold became stricter (Table 1). Thus, the more liberal threshold of 5 mm is more inclusive for difficult-to-image child populations, while a stricter criterion would be impractical.

Yet, it must be ruled out that the tendency for children to move their heads more so than adults may have driven the differences in BOLD activation. To address this concern, the BOLD signal change for crossmodal processing—the combined dependent measure of VH and HV that produced the largest effect—was compared to mean motion

in each group. Results indicated that the correlation between these two measures was not significant in either age group (7 to 8.5 year olds: ($r^2(9) = 0.070$, $p = n.s.$); adults: ($r^2(8) = 0.172$, $p = n.s.$)). Based on these findings, it is unlikely that the differences in neural activity can be accounted for by head motion.

3.3. Results

3.3.1. Sample encoding phase

3.3.1.1. Overlapping maps of activation

Statistical Parametric Maps (SPMs) revealed overlapping areas of visual and haptic encoding in adults and 7 to 8.5 year olds (Fig. 5A-E). Several whole brain contrasts were used during the sample encoding phase to indicate regions of activation for vision (VV + VH > rest; blue tones) and for haptics (HH + HV > rest; red tones). These contrasts are shown separately in the adults and in the 7 to 8.5-year-old children. As expected in adults, vision and haptics showed overlapping areas of activation bilaterally in the LOC, as well as in the IPS (IPS partially shown; Fig. 5A). Similarly in children, activation for vision and haptics overlapped bilaterally in the LOC and the IPS (Fig. 5B). Direct comparison of the two age groups found no significant clusters, indicating very similar regions of neural activity during haptic sample encoding—the overlap between adults and 7 to 8.5 year olds encompassed bilateral areas in the LOC and the IPS (Fig. 5C). During visual sample encoding, both age groups showed bilateral activity in the LOC (Fig. 5D) and, similar to haptics, there were no significant differences between groups. In both haptic and visual sample encoding analyses, there was a trend for children's activation to be more widespread than adults (see supplementary Fig. S1).

3.3.1.2. Differences between maps of activation

Complementary to the overlap analysis just described, whole-brain contrasts were also used to examine the *differences* between visual and haptic sample encoding in adults and in 7 to 8.5 year olds (Figs. 6-7). In these figures, regions of neural activity in which vision was greater than haptics (VV + VH > HH + HV) are depicted in blue (adults) and light blue (7 to 8.5 year olds); regions in which haptics was greater than vision (HH + HV > VV + VH) are depicted in orange (adults) and yellow (7 to 8.5 year olds). In adults, visual sample encoding activated areas of visual cortex bilaterally (Fig. 6A, Z = -4), while haptic sample encoding activated bilateral areas in the IPS (Fig. 6A, Y = -67, top). Similar patterns of activation were found in 7 to 8.5 year olds (Fig. 6B). Critically, results indicated bilateral middle temporal/occipital regions (MTG/MOG) in the putative visual cortex that showed significantly greater activity for *haptics* than for vision in both age groups (Fig. 6; see Fig. 7 for a 3D depiction, lateral views). These haptic-biased regions in MTG/MOG did not overlap with the bimodal regions described above, suggesting a haptic-preferring region in the visual stream that is not part of LOtv. Examining the overlap and difference maps together revealed a medial to lateral transition from a visual bias in activation on the medial fusiform gyrus (FG) to a haptic bias in activation on the MTG/MOG, with the bi-modal LOtv region in between on the lateral occipitotemporal sulcus (see Fig. 8A). This transition is further illustrated in a gradient of visual to haptic biases during the sample encoding phase (displayed on "flooded" maps in Fig. 8B); a similar pattern was present during the test matching phase (Fig. 8C).

3.3.2. Test matching phase

3.3.2.1. Whole brain activation

A balanced contrast comparing the experimental conditions against rest (i.e., (VV + HH + VH + HV > rest)) during the test matching phase also revealed known multisensory visuohaptic substrates in children and adults, including the LOC and the IPS (Fig. 9A; Amedi et al., 2001, 2002, 2005; Jao, James, & James, 2014; James et al., 2002; James & Kim, 2010; Stilla & Sathian, 2008). Based on these whole-brain results, the network of neural substrates underlying visuohaptic processing appears to be recruited not only in adults, but importantly, are similarly activated in children by 7 years of age for this task.

To reveal specific effects of crossmodal enhancement throughout the brain, we compared crossmodal to intramodal matching using a conjunction of two contrasts, namely, the crossmodal haptic-to-visual matching task versus both intramodal tasks (i.e., (HV > VV) ∩ (HV > HH); Fig. 9B). This is similar to an intersection contrast in a PET study performed by Hadjikhani and Roland (1998), who discovered activation in the insula-claustrum only and suggested that this region must play a crucial role in the integration of crossmodal inputs. While we did not find activation in this region with our contrast (see Remedios, Logothetis, & Kayser, 2010 for evidence against the claustrum as an integrator of sensory information), we did find activation in the LOC bilaterally that overlapped across children and adults. The analogous intersection contrast with crossmodal visual-to-haptic matching (i.e., (VH > VV) ∩ (VH > HH)) showed a less stable pattern. The only cluster was found in the postcentral gyrus in adults, but a contrast across groups did not reveal a significant difference in this region.

3.3.2.2. Region-of-Interest results

To assess the pattern of activation during the test matching phase in the LOC ROI (see Fig. 5E, green arrow for overlapping contrasts used to define the ROI; Table 2), a

repeated measures (2 x 2 x 2) ANOVA was performed on the data extracted from that ROI (Fig. 10A) with test modality (visual or haptic) and test trial type (intramodal or crossmodal) as the within-subjects factors, and age group (7 to 8.5 year olds or adults) as the between-subjects factor. Results indicated a main effect of test trial type ($F(1,19) = 11.992$, $p = .003$; Fig. 10B), with greater response for crossmodal than intramodal processing overall ($t(20) = 3.562$, $p = .002$). This crossmodal enhancement effect was present in 7 year olds ($t(10) = 2.344$, $p = .041$), as well as in adults ($t(9) = 2.680$, $p = .025$). Furthermore, there was a main effect of group ($F(1,19) = 5.308$, $p = .033$). Adults showed significantly higher BOLD signal change than 7 to 8.5 year olds for each test trial type (intramodal: ($t(19) = 2.191$, $p = .041$); crossmodal: ($t(19) = 2.138$, $p = .046$)). There was no main effect of modality at test, however, suggesting fairly equivalent processing of both visual and haptic inputs in this region during the matching of objects for recognition (Fig. 10C). Interestingly, adults showed significantly higher BOLD signal change than 7 to 8.5 year olds during the visual test modality ($t(19) = 2.391$, $p = .027$). This result supports previous findings in which the LOC becomes increasingly visually dominant with development, particularly for object-preference (Jao, James, & James, 2014).

To examine the activation patterns in the medial FG and lateral MTG/MOG ROIs, particularly in relation to the overlapping LOC ROI during the test matching phase (Fig. 8A, 8C; Table 2), a repeated measures (2 x 2 x 2 x 3) ANOVA was performed with age group (7 to 8.5 year olds or adults) as the between-subjects factor, and test modality (visual or haptic), test trial type (intramodal or crossmodal), and ROI (medial, overlap, lateral) as the within-subjects factors. Results showed a main effect of age group ($F(1,19)$

= 8.895, p = .008), with significantly higher BOLD signal change overall in adults than in 7 to 8.5 year olds (t(19) = 2.982, p = .008), as well as a main effect of ROI (F(2,18) = 7.398, p = .005). The statistical comparisons shown in Fig. 11 are within each age group and separated by region. Further results indicated a test type x ROI interaction effect (F(2,18) = 4.148, p = .033); there was a greater response for crossmodal than intramodal processing within each group (7 to 8.5 year olds: (t(10) = 2.344, p = .041); adults: (t(9) = 2.680, p = .025)) in the overlapping LOC ROI (Fig. 11B, top; also see Fig. 10B). This crossmodal enhancement effect, however, was not present in either age group in the medial FG ROI (Fig. 11A, top) or the lateral MTG/MOG ROI (Fig. 11C, top). Finally, there was a test modality x ROI interaction effect (F(2,18) = 49.064, p < .001). In the medial ROI, BOLD responses were significantly higher when processing visual than haptic inputs in each group (7 to 8.5 year olds: (t(10) = 4.264, p = .002); adults: (t(9) = 4.330, p = .002); Fig. 11A, bottom). In the overlap ROI, there were no significant differences between visual and haptic processing (Fig. 11B, bottom; see also Fig. 10C). Lastly, in the lateral ROI, BOLD responses were higher when processing haptic than visual inputs in each group (7 to 8.5 year olds: (t(10) = 2.536, p = .030); adults: (t(9) = 6.213, p < .001); Fig. 11C, bottom).

3.4. Discussion

The present study used functional MRI to investigate the development of crossmodal visuohaptic object recognition. The main finding was that visuohaptic crossmodal matching produced greater activation than intramodal matching in the LOC for both adults and children. To our knowledge this is the first study to find this effect in the LOC

in adults or children. The key developmental finding was that children from 7 to 8.5 years of age did not differ qualitatively in terms of the overall pattern of activation, even though children did produce less activation in general across all conditions in the LOC during test matching. Additionally, the data revealed a novel finding of a haptic-preferring region in the bilateral middle temporal/occipital gyrus, a putative visual region, that was not considered "bimodal." A broader perspective showed that the ventral occipitotemporal cortex followed a medial to lateral organization with a visual to bimodal to haptic pattern of activation that was present in both age groups. Although the LOC is a known region of visuohaptic convergence, these results provide novel insights into the mechanisms invoked for sequential information sharing across sensory modalities, as well as into the development of those mechanisms.

3.4.1. Developmental similarities and differences

Both adults and children showed crossmodal enhancement effects, and recruited similar multisensory systems during visuohaptic object recognition. Neural activity in children, however, was generally more widespread during sample encoding, and weaker within a specialized bimodal area (i.e., the LOC) during test matching, than in adults. This suggests that although the neural mechanisms supporting crossmodal visuohaptic object processing are in place by 7 years, they are still undergoing change. According to psychophysical findings, children aged 8 to 10 years begin to appear adult-like in terms of integrating visual and haptic information for certain aspects of form discrimination (e.g., size and orientation; Gori et al., 2008). Prior to this age, however, children were shown to be unable to combine sensory information for perception in an optimal manner. These behavioral results suggest that there is a "transitional" stage of development prior

to 8 years during which visuohaptic integration for specific types of shape discrimination becomes optimized. There is also prior neural evidence that the LOC continues to develop after 7 years of age with continued experience on some visual or visuohaptic tasks. For instance, previous work has shown that visual dominance in the LOC during visuohaptic object recognition does not reach adult levels until after 8.5 years (Jao, James, & James, 2014). More specifically, it was found that visual dominance in the LOC continued to increase from 8.5 years of age into young adulthood, while activation for the haptic modality remained fairly constant from 4 years into adulthood. This finding was replicated in the current study in which BOLD activation for vision was higher in adults than in children during the test matching phase.

The age ranges for the current study were therefore selected with the expectation that the fMRI data would follow the patterns seen in previous studies, that is, a transitional, non-optimal level of multisensory integration in children as compared to adults. This was indeed the case, as children not only showed more widespread whole-brain activity than adults during sample encoding, they also showed lower levels of BOLD activation in the LOC during test matching for crossmodal and intramodal processing. The selection was also based to some degree on the ability of children at different ages to perform the delayed match-to-sample tasks successfully, which required the participants to maintain the sample stimulus in memory during each of the subsequent matching trials. In the current study, all of the 7 to 8.5-year-old children were able to do so successfully. While testing an even younger age range may provide further details about the developmental trajectory of visuohaptic integration, the current findings are interpretable in their own right.

3.4.2. Haptic-preferring regions within the LOC

Contrasts of vision versus haptics revealed robust effects in both age groups in which bilateral regions in the occipitotemporal cortex showed greater activity for haptics than for vision. While other studies have found haptic object-selectivity—often defined by a contrast of haptic shape versus haptic texture—in the LOC (Amedi et al. 2001; Lacey, Flueckiger, Stilla et al., 2010; Stilla and Sathian 2008; Zhang et al. 2004; Stoesz et al. 2003; Prather et al. 2004; Peltier et al., 2007; for a review, see Lacey et al., 2009), it has always been found to be overlapping with visually object-selective regions (Amedi et al., 2001; James et al., 2002; Stilla and Sathian 2008; Peltier et al., 2007; among others). Thus, ours is the first study to our knowledge that has reported a region in the ventral "visual" stream that responds significantly more during haptic than visual processing. This may be due to the majority of the aforementioned studies emphasizing the overlap of haptics and vision, rather than the difference between the two sensory modalities. There have, however, been indications of this pattern in adults in at least one previous study. Amedi and colleagues (2001) showed that somatosensory shape processing not only activated a region of the occipitotemporal cortex that overlapped a subregion of the visual LOC, namely in the LOtv, it also activated regions abutting the LOtv.

The current findings may not simply be the result of contrasting vision and haptics, however; they may be due to the context of the encoding phase, which was the sample phase of a crossmodal delayed match-to-sample task. Within the context of crossmodal object recognition, children and adults may be encoding the sample in such a way that haptic processing activates an additional region within the ventral occipitotemporal cortex that is driven more by haptics than by vision, although this region may not necessarily be object-

selective. This hypothesis seems even more likely given that the participants knew beforehand whether the sample stimulus was to be matched to a crossmodal or intramodal target. Although this was an unexpected finding, it warrants further investigation, especially as it relates to the malleability of putative visual cortical signals by task demands.

Examining the whole of the ventral occipitotemporal cortex, the overlapping patterns of visual and haptic activation during sample encoding and test matching showed a medial to lateral transition from a visual to haptic bias in the mapping of the sensory modalities used to process shape information. The mapping transitioned from regions of visual preference that were located more medially to regions of haptic preference that were located more laterally, with bimodal visuohaptic preference in the overlapping middle regions. Although not widely reported in the literature, there has been mention of a similar trend in at least one previous study. Specifically, whole-brain results of haptic and visual shape-selectivity showed the recruitment of bilateral regions that were each adjacent to the overlapping bimodal area in the LOC and opposite to one another, thus following a similar transition pattern (Stilla & Sathian, 2008). Finding a haptic-preferring region in the LOC suggests that the multisensory signals integrated in the LOtv likely arrive via neighboring modality-biased regions within the LOC itself. We hypothesize that these modality-biased regions transform somatosensory and visual signals to facilitate multisensory integration in the LOtv. A future step should be identifying the exact nature of those transformations.

3.4.3. Crossmodal effects in the LOC

3.4.3.1. Crossmodal enhancement over intramodal matching

Crossmodal haptic-to-visual matching, which required the subject to compare visual test

stimuli with the haptic sample, activated the LOC—a putative visual region—more strongly than the intramodal control conditions. The region of LOC that showed this effect overlapped in children and adults. Thus, in accordance with our first prediction, there was a stronger response for crossmodal than intramodal matching that was apparent in both age groups. This effect, however, was present only for haptic-to-visual crossmodal recognition; contrasting visual-to-haptic crossmodal matching with intramodal conditions did not yield a significant effect in the LOC. This asymmetry is discussed in the next subsection (3.4.3.2. Crossmodal asymmetry). The ROI analysis revealed that, within each type of condition, adults showed higher levels of BOLD activity than 7 to 8.5 year olds. Thus, both intramodal and crossmodal processing are still developing in children, which reflects a decreased ability to process visual and haptic information about object shape. Additionally, the crossmodal enhancement effect was present in the overlapping bimodal LOC region (LOtv), but not in the medial visual-preferring or lateral haptic-preferring areas of the LOC. Together, these results suggest that the LOC not only processes crossmodal information, but also more importantly, is sensitive to sequential *changes* in sensory modality during object recognition.

One possible explanation for the crossmodal enhancement effect is the reactivation of the encoded object at test that occurs in parallel with the activation of the test object. The LOC, as a multisensory region concerned with determining object shape, processes visual and haptic inputs in parallel. In situations in which information from one modality or another is unavailable, it must be able to detect any changes in sensory input and share the accessible information between modalities efficiently. Much of the research conducted on visuohaptic processing has now established that the LOC is bimodal in

terms of its representations of visual and haptic (familiar and novel) shape information (Amedi et al., 2001; James et al., 2002, 2005; James & Kim, 2010; Lacey et al., 2010, 2014; Peltier et al., 2007; Pietrini et al., 2004; Stilla & Sathian, 2008; Stoesz et al., 2003; Zhang et al., 2004), and the current data also support this notion. Moreover, a recent study has demonstrated neural convergence of visual and haptic inputs in the LOC through inverse effectiveness (Kim, Stevenson, & James, 2012). Based on these findings, it is plausible that during crossmodal recognition, some of the population of neurons within this region would be reactivated at test (see Lacey & Sathian, 2014 for a review of mental imagery), while others would be activated by the sensory percept. The combination of activated and re-activated neural populations would produce greater activation in crossmodal matching tasks, which require reactivation of the encoded stimulus as well as activation for the current sensory input, than in intramodal matching tasks, which do not. Furthermore, this notion corroborates previous findings from an fMRI-based adaptation paradigm used to examine the characteristics of specific neuronal populations, which indicated increased proportions of bimodal neurons and clear crossmodal repetition suppression effects in the LOtv (Tal & Amedi, 2009).

Alternatively, it is possible that the crossmodal tasks may simply have been more difficult and required more intense processing than the intramodal matching tasks. While this is possible in the current study and should be addressed in future studies, the presence of a weak asymmetry in activation between the two crossmodal conditions seems to indicate that difficulty alone cannot explain the differences.

3.4.3.2. Crossmodal asymmetry

While the present findings indicated crossmodal enhancement effects in the LOC, direct

comparisons of crossmodal conditions (i.e., VH vs. HV) during the test matching phase did not provide strong evidence for an asymmetry, or two-way directionality effect, of crossmodal processing. Comparisons between the HV and VH conditions indicated no significant differences in children or adults.

Although asymmetries within crossmodal processing have been addressed in previous studies, these have resulted in varying conclusions. In one particular study, Positron Emission Tomography (PET) was implemented to examine the effects of the presentation order of crossmodal information (Kawashima et al., 2002). Using crossmodal discrimination tasks in conditions analogous to the current study (i.e., visual-to-haptic, haptic-to-visual), their findings showed asymmetric processing of crossmodal stimuli such that only the visual-to-haptic presentation order activated the inferior temporal cortex, while both presentation orders activated the inferior parietal cortex. It was proposed that this was evidence for two different pathways underlying crossmodal discrimination depending on the temporal order of stimulus presentation (Kawashima et al., 2002). Similar types of directionality effects have been demonstrated very recently in bilateral regions of the lateral occipital cortex and the aIPS using fMRI, but have only been found in one direction (Kassuba et al., 2013). This asymmetry during crossmodal matching occurred only in congruent visual-to-haptic conditions, with little effect of crossmodal matching on brain activation in these regions during incongruent or haptic-to-visual conditions. Based on these results, Kassuba and colleagues (2013) concluded that there is a modality-specific asymmetry with a preference supporting the functional primacy of vision during visuohaptic object recognition.

The present study, however, did not find evidence for this functional primacy of

vision. Rather, the whole-brain results from the test matching phase indicated the opposite effect in which haptic-to-visual crossmodal recognition activated the LOC in both adults and children, while visual-to-haptic recognition had little effect in either age group. To examine this further, direct comparisons were made in the post-hoc ROI analysis, but results indicated no significant differences between the HV and VH conditions. As such, while it is possible that crossmodal processing in the LOC may be constrained by the dominant modality that provides the most salient or reliable of information at the time of recognition (i.e., vision)—which would be consistent with models of optimal integration where each sensory modality is weighted according to its reliability (Ernst & Banks, 2002; Helbig & Ernst, 2007)—our findings are not strong enough to support (or refute) this pattern of asymmetry. Nevertheless, the current findings lend support for the notion that the recruitment and specific location of multisensory convergence areas is highly contingent upon two primary factors: the information content being processed (e.g., shape), and the modality being used to process the crossmodal input during recognition (Amedi et al., 2005).

Overall, the current results and findings from previous studies seem to indicate that multisensory integration cannot be described as a unitary developmental process, but instead should be described as several processes that follow differing developmental timelines. Some processes such as crossmodal recognition may require more experience in order to be optimized, and thus take longer to fully develop than others depending on the types of input being processed. In terms of visual processing, prior behavioral evidence has shown that even children from 6 to 8 years have difficulty recognizing objects from unusual views (Bova et al., 2007; Juttner et al., 2006; Mondloch et al., 2003;

Mondloch, Le Grand, & Maurer, 2002; see Nishimura, Scherf, & Behrmann, 2009 for a detailed review), and are relatively poor compared to adults at recognizing complex forms such as faces (Mondloch, Maurer, & Ahola, 2006; although see Crookes and McKone, 2009). These delays in specific visual object recognition proficiencies implicate a delayed development of the occipitotemporal cortex, particularly of the LOC, but perhaps only for more specific types of shape processing. Thus, the processing of complex objects or abstract forms of inputs (e.g., crossmodal stimuli) may result in protracted developmental trajectories as compared to the processing of simple shapes. Studying the development of these processes constitutes grounds for future research.

3.4.4. Handedness and the LOC

Bimanual exploration, which was implemented in the current study, may obviate the need to control for handedness. Activation in higher-level cortical regions such as the LOC appear not to be influenced by the hand used during exploration. Previous fMRI findings comparing left- and right-handed object exploration have shown bilateral LOtv activity that was not influenced by the hand-in-use (Amedi et al., 2010). Moreover, results from further studies have shown a left-lateralized bias in activation with either left-handed exploration (James et al., 2006; Kilgour et al., 2005), right-handed exploration (Kim, Stevenson, & James, 2012), or bimanual exploration (Kim & James, 2010).

Based on this body of evidence, there is a possibility that while the hand-in-use may not contribute much to the neural response in higher cortical areas during visuohaptic object exploration, general handedness may (Kim, Stevenson, & James, 2012). Specifically, the left-lateralized bias found in the LOC may be due not to the hand used to explore the stimulus, but rather to the strong right-handed preference of the

participants tested in these studies. Thus, to minimize differences in handedness preference, we recruited mostly right-handed participants, and did not include any strongly left-preferring participants.

3.4.5. Conclusions

In summary, using a crossmodal delayed match-to-sample task with novel objects, we have investigated the neural substrates involved in visuohaptic processing in children and adults. Importantly, we argued that there is crossmodal enhancement in the LOC, suggesting that this region is sensitive to *changes* in sensory modality. We have shown that this effect, as well as the network of multisensory regions consistently found in adults, is present in children by 7 years of age, although children show generally more widespread activity during sample encoding and weaker BOLD signal change in the LOC during test matching than adults. Finally, we have found novel evidence of a bilateral region in the MTG/MOG that is haptic-preferring in both age groups. This region abuts the bimodal LOtv, and indicates a medial to lateral, visual to haptic, transitional bias in the LOC.

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Table 1. Number of subjects retained at different motion tolerance thresholds.

Motion Threshold	Total No.	7 to 8.5 years	Adults
5 mm	21	11	10
4 mm	21	11	10
3 mm	17	7	10
2 mm	17	7	10
1 mm	13	3	10

Table 2. Talairach coordinates (*x*, *y*, *z*), peak *t*-values, *p*-values, and number of voxels for the overlap, medial, and lateral ROIs at test.

Region	*x*	*y*	*z*	*t*-value	*p*-value	No. of Voxels
Overlap: LOC	-49	-65	-6	4.346	.001	756
Medial: FG	-37	-71	-15	3.759	.001	618
Lateral: MTG/MOG	-53	-62	6	4.127	.001	578

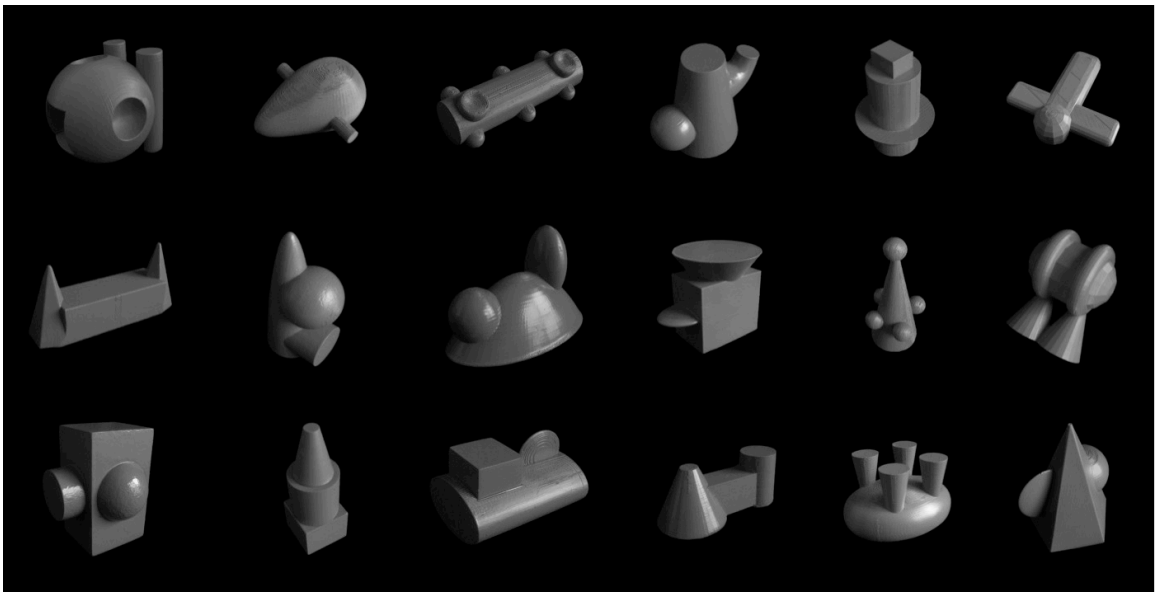

Figure 1. Subset of novel stimuli used in the present study. Objects are not to scale.

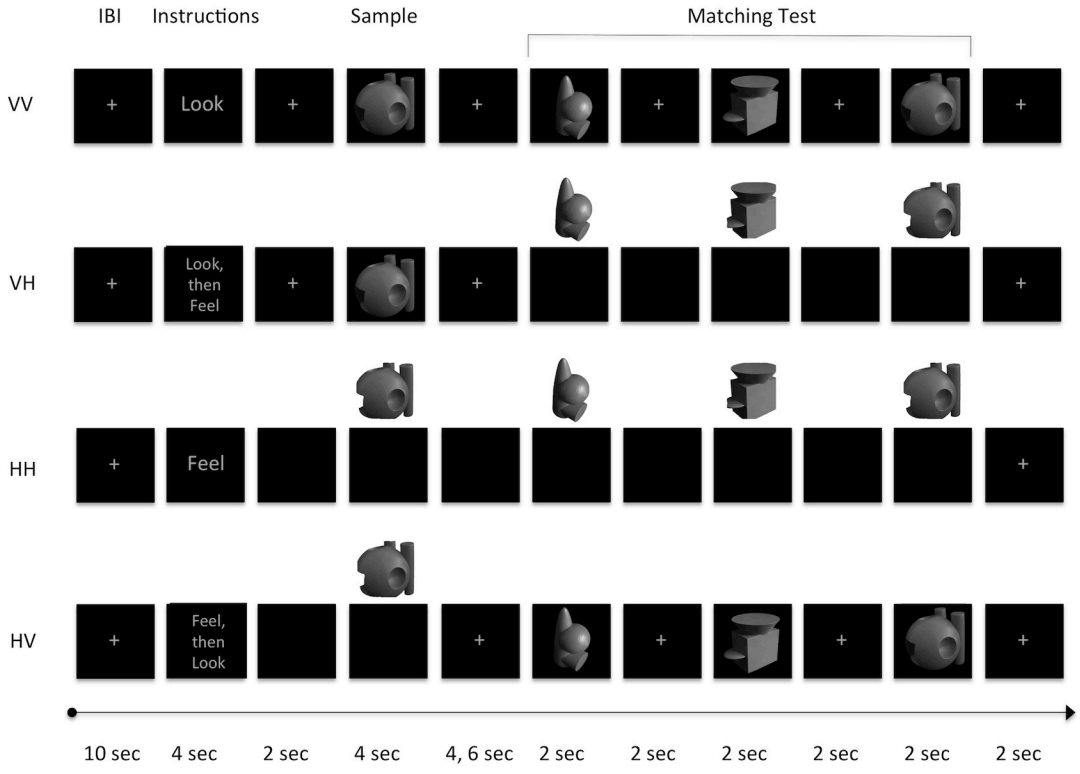

Figure 2. Graphical depiction of the fMRI mixed event-related/block design. This figure demonstrates the timing protocol of a single trial set for each condition.

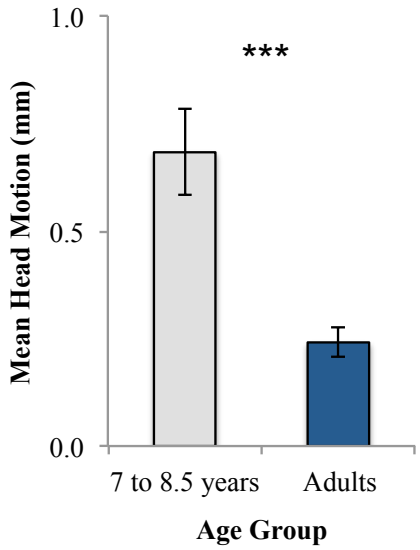

Figure 3. Mean head motion (in mm) for each age group. On this and subsequent figures, error bars represent standard error of the mean; significant differences at $p < .001$ are depicted with ***, $p < .01$ with **, and $p < .05$ with *.

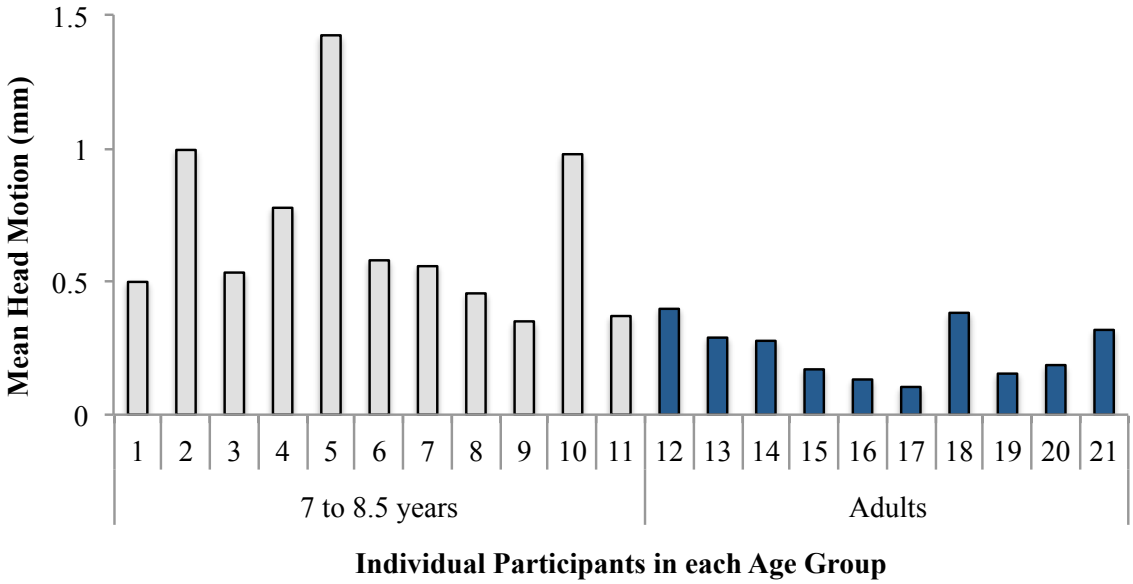

Figure 4. Mean head motion (in mm) for each individual participant within each age group.

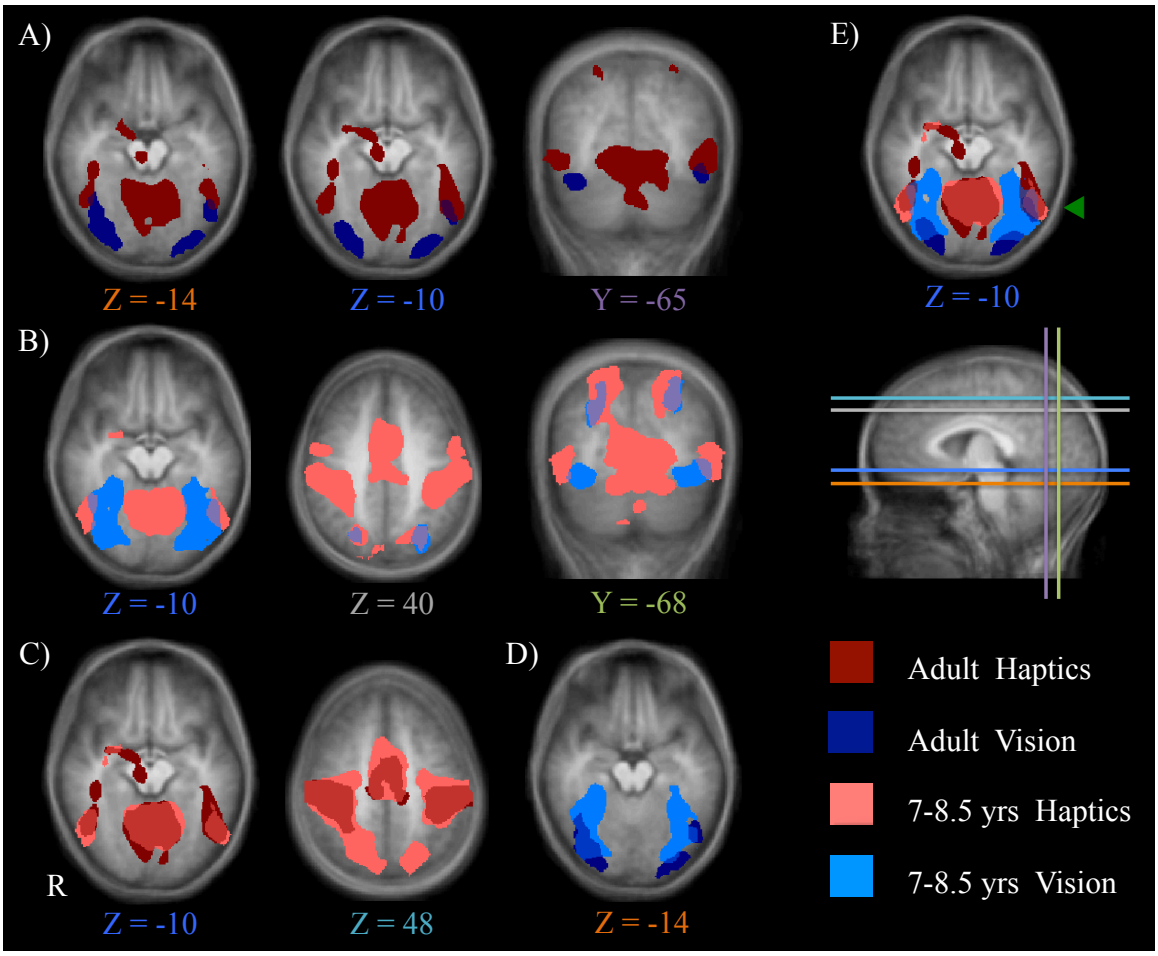

Figure 5. Sample encoding phase: Whole-brain overlap maps. Statistical Parametric Maps (SPMs) of group contrasts show overlapping areas of activation. A) Overlap between vision (VV + VH > rest, balanced; navy blue) and haptics (HH + HV > rest, balanced; dark red) in adults. B) Overlap between vision (VV + VH > rest, balanced; light blue) and haptics (HH + HV > rest, balanced; salmon) in 7 to 8.5 year olds. C) Overlap between adults (dark red) and 7 to 8.5 year olds (salmon) for haptics (HH + HV > rest, balanced). D) Overlap between adults (navy blue) and 7 to 8.5 year olds (light blue) for vision (VV + VH > rest, balanced). E) Overlap between A-D for the LOC ROI selection (green arrow). On this and subsequent figures, colored lines on the sagittal plane correspond to axial slices along the z-axis and coronal slices along the y-axis. Functional data are presented at a threshold of $p < 0.05$ (corrected) on an averaged T1-weighted anatomical image of all participants.

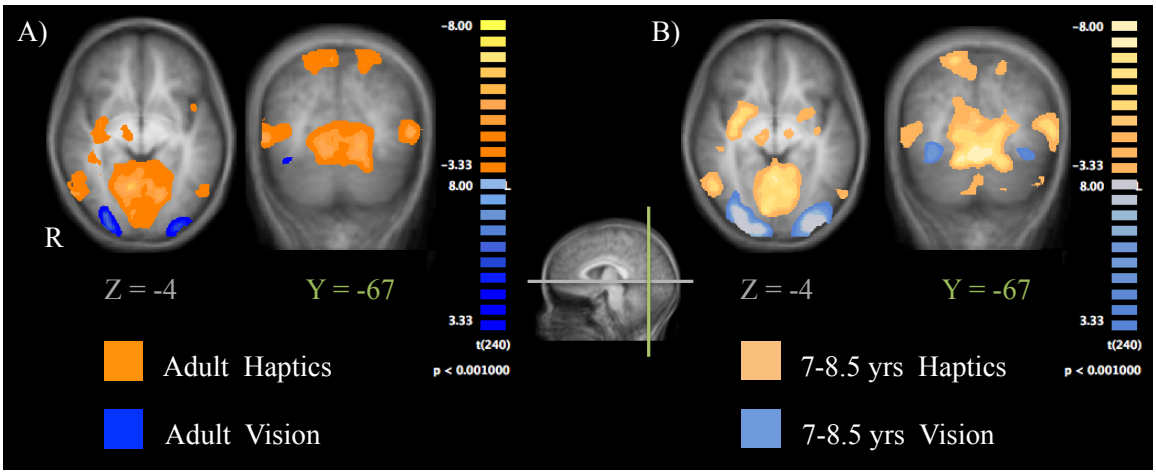

Figure 6. Sample encoding phase: Whole-brain difference maps. SPMs of statistical differences between vision and haptics during the sample encoding phase in: A) adults; and B) 7 to 8.5 year olds. Regions showing significantly greater activity for haptics than vision (HH + HV > VV + VH) is depicted in orange (adults) and yellow (7 to 8.5 year olds). Regions showing significantly greater activity for vision than haptics (VV + VH > HH + HV) is depicted in blue (adults) and light blue (7 to 8.5 year olds).

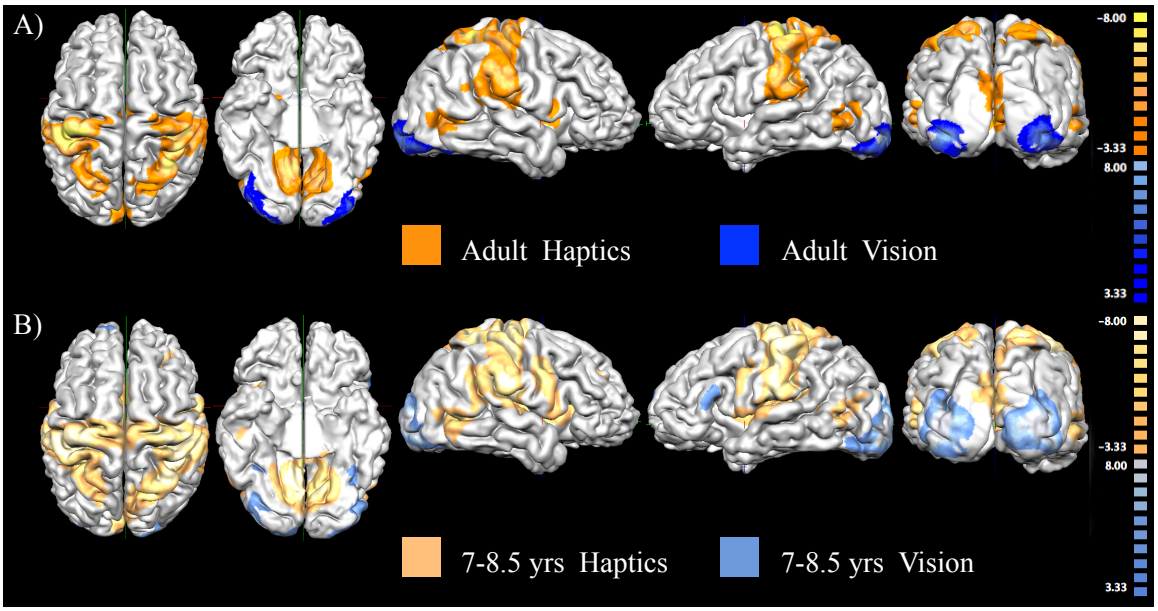

Figure 7. Sample encoding phase: Overall difference. Statistically significant differences between vision and haptics during the sample encoding phase in: A) adults; and B) 7 to 8.5 year olds. Significant areas of activation for haptics (HH + HV > VV + VH) are shown in orange (adults) and yellow (7 to 8.5 year olds), as compared to areas of activation for vision (VV + VH > HH + HV), which are shown in blue (adults) and light blue (7 to 8.5 year olds). Views from left to right: superior, inferior, right hemisphere, left hemisphere, and posterior. Statistical maps are overlaid on a representative 3D anatomical image.

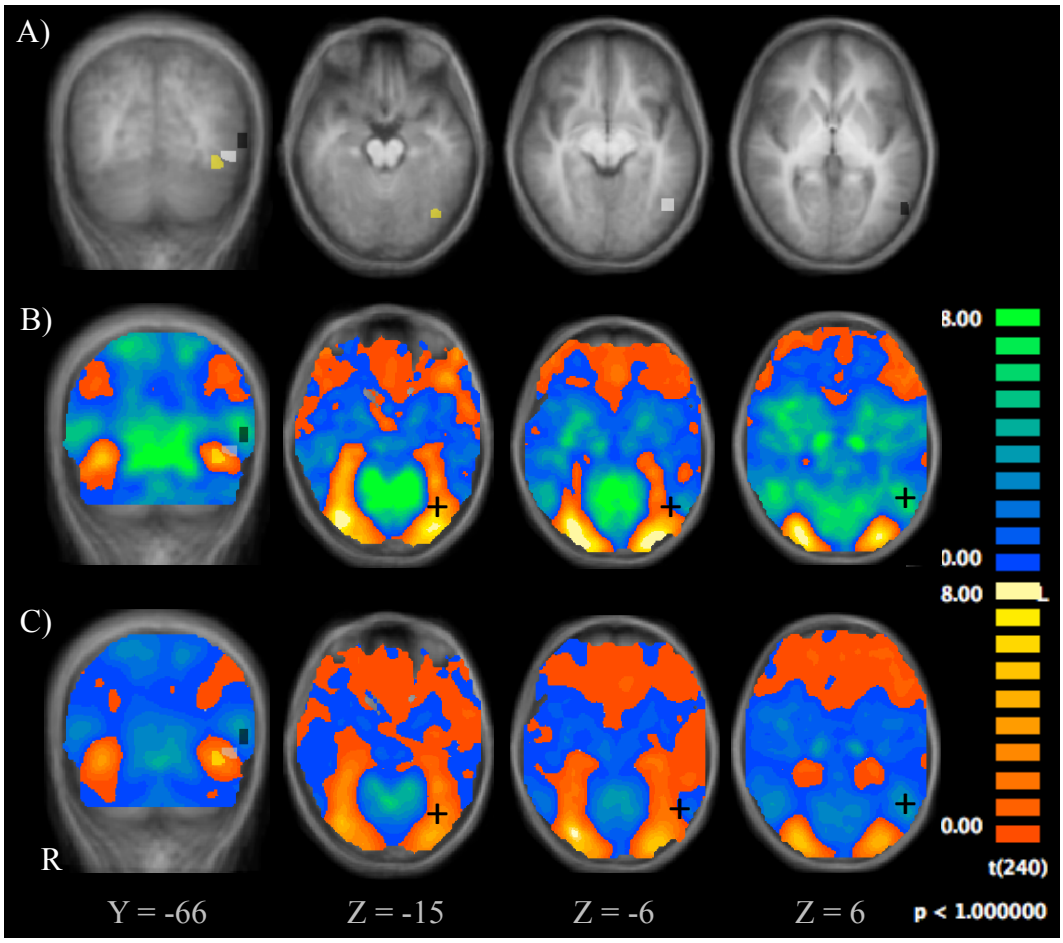

Figure 8. Medial to lateral transition. A) Locations of the medial FG ROI (yellow), overlap LOC ROI (gray), and lateral MTG/MOG ROI (black). B) Flooded SPMs (VV + VH > HH + HV) show a gradient of visual (orange) to haptic (green) biases from medial to lateral regions during the sample encoding phase in all participants. C) Flooded SPMs (VV + HV > HH + VH) show a similar gradient during the test matching phase; crosshairs indicate ROI peaks. Crosshairs in B are for reference only.

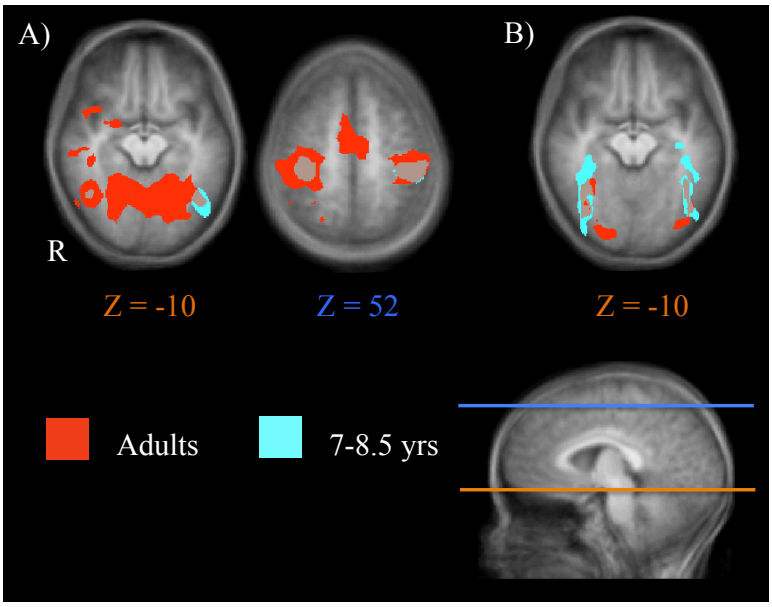

Figure 9. Test matching phase: Whole-brain maps. A) SPMs of group contrasts between all conditions versus rest (VV + VH + HH + HV > rest, balanced). Crossmodal and intramodal matching in children and adults activated an overlapping network of regions that has been shown to be involved in multisensory visuohaptic object recognition. Regions include the LOC (Z = -10) and the IPS (Z = 52). B) Crossmodal as compared to intramodal matching. SPM of the conjunction contrast for haptic-to-visual matching as compared to visual-only and haptic-only matching (i.e., (HV>VV) ∩ (HV>HH)) activated the LOC bilaterally (Z = -10) and overlapped between children and adults. Data from adults (red) and children (blue) are presented at a threshold of $p < 0.05$ (corrected). LOC = lateral occipital complex; IPS = intraparietal sulcus.

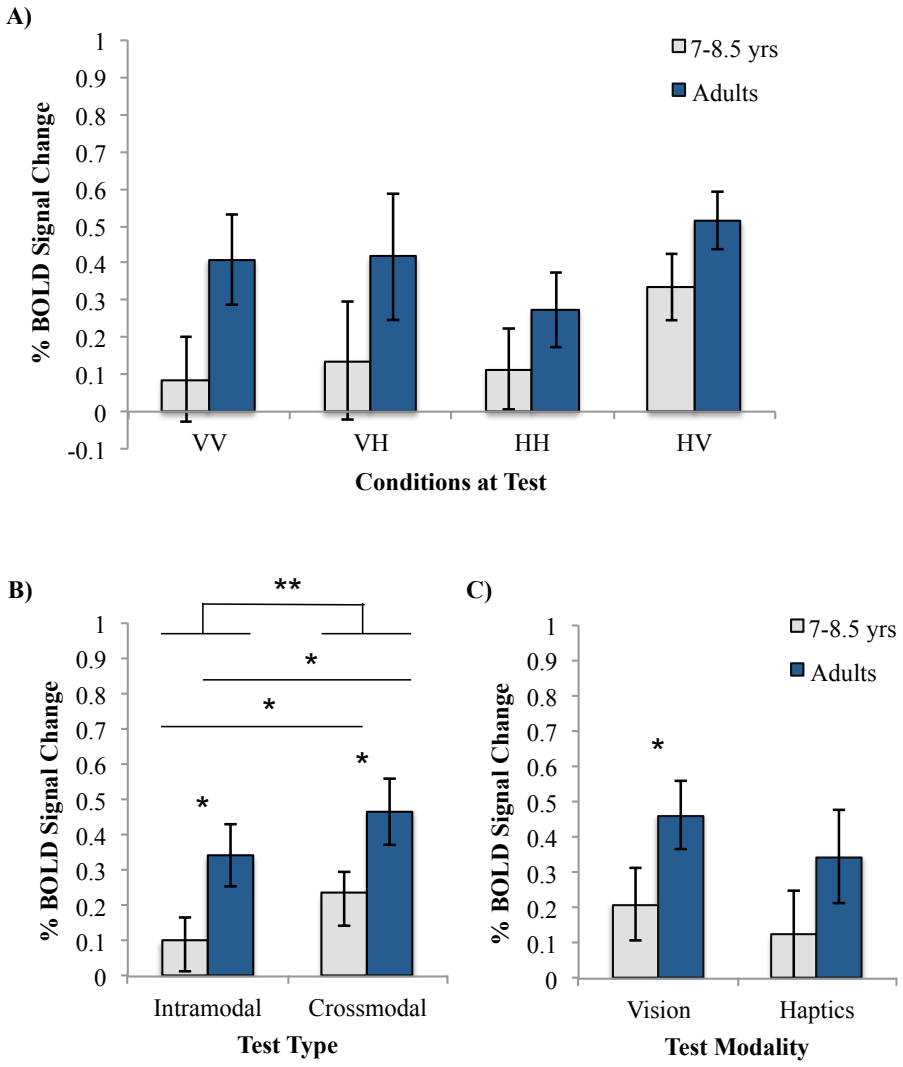

Figure 10. Test matching phase: LOC ROI. Percentage BOLD signal change from the group-based ROI is presented for each group of participants during the test matching phase for: A) overall conditions; B) test type (intramodal: VV and HH; crossmodal: VH and HV); and C) test modality (vision: VV and HV; haptics: HH and VH).

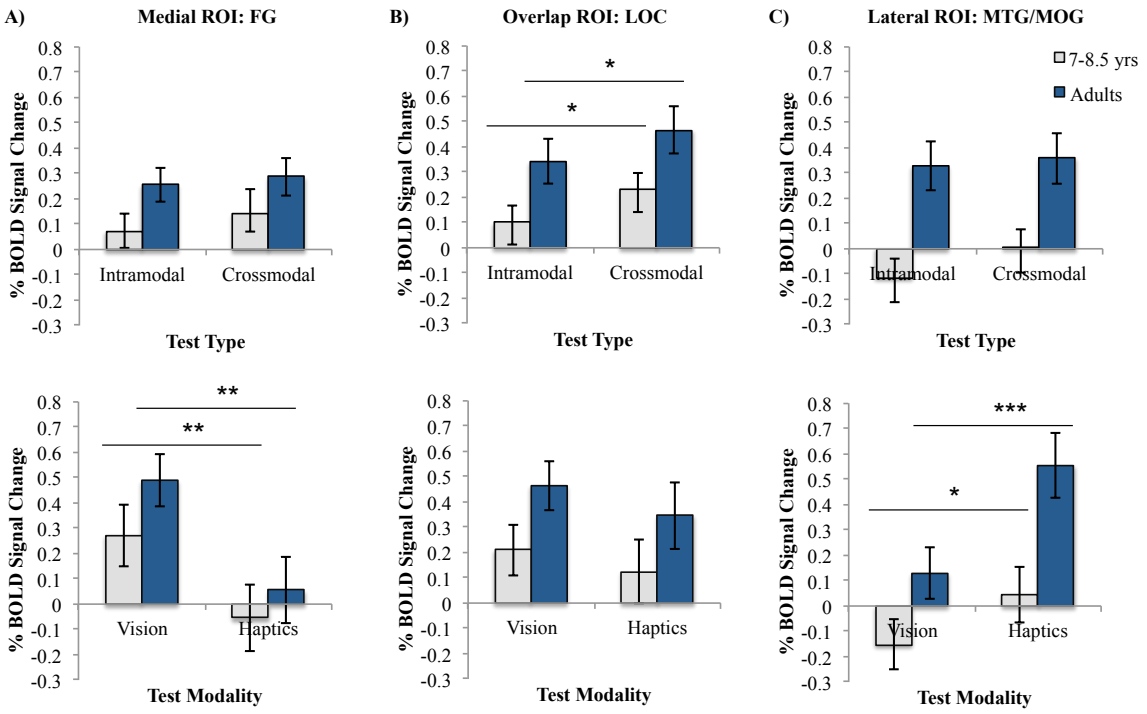

Figure 11. Test matching phase: Medial to lateral ROIs. Percentage BOLD signal change during the test matching phase is presented for each group of participants. Comparisons within test type (intramodal: VV and HH; crossmodal: VH and HV) and test modality (vision: VV and HV; haptics: HH and VH) are shown for the group-defined: A) medial ROI (FG); B) overlap ROI (LOC); and C) lateral ROI (MTG/MOG).

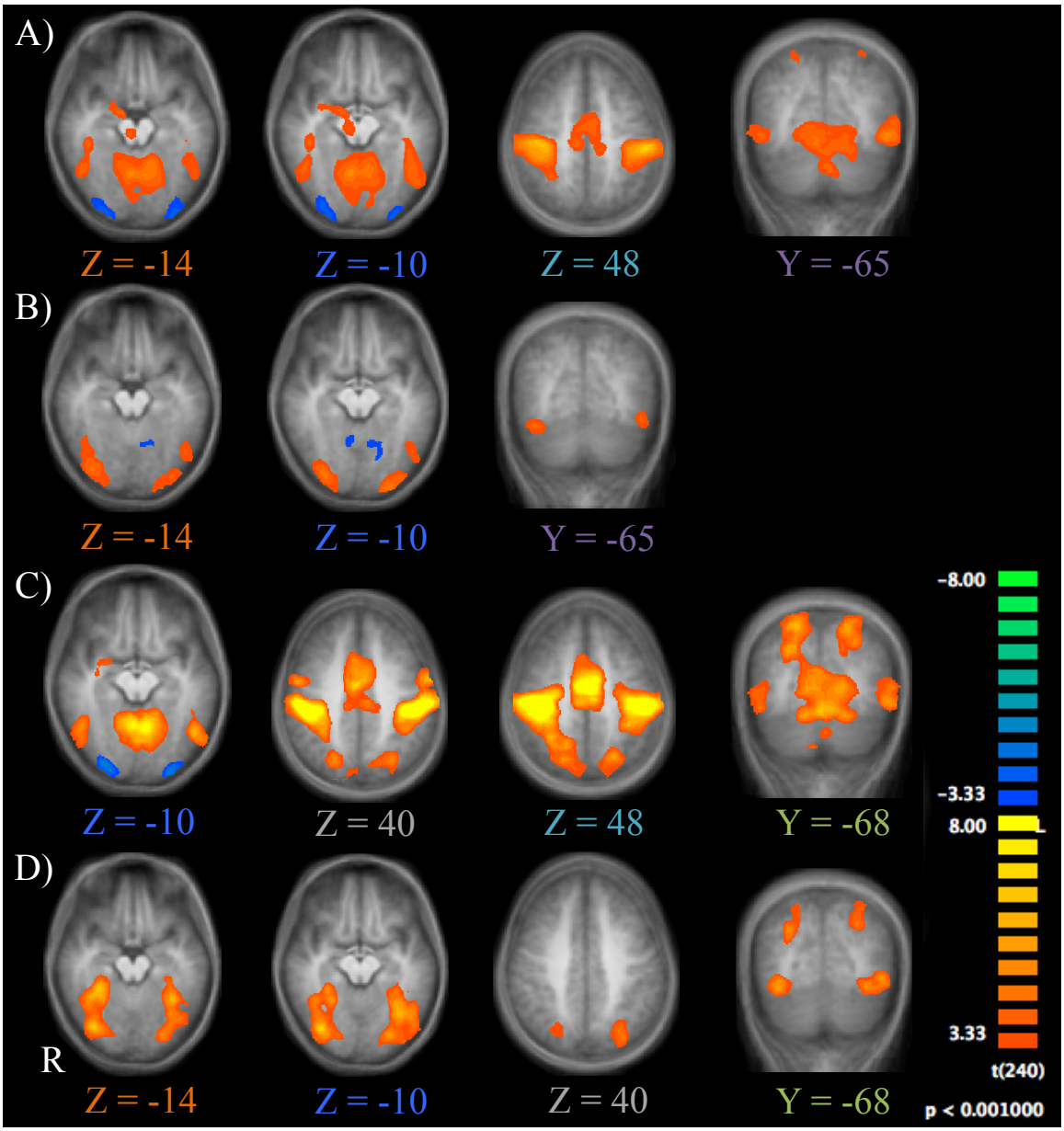

Figure S1. Sample encoding phase: Whole-brain activation maps. Statistical Parametric Maps (SPMs) show the strength of activation for: A) adult haptics (HH + HV > rest, balanced); B) adult vision (VV + VH > rest, balanced); C) 7 to 8.5 year old haptics (HH + HV > rest, balanced); and D) 7 to 8.5 year old vision (VV + VH > rest, balanced). These maps for each group and each modality form the whole-brain overlap maps (see Fig. 5A-D).

Chapter 4.

Developmental Changes in Visuohaptic Functional Connections Between the Dorsal and Ventral Streams

Abstract

Vision and haptics are two modalities predominantly used to interact with the surrounding environment, as well as the objects within it. These modalities are oftentimes combined, through multisensory convergence or integration, to aid in this interaction. Two particular brain regions implicated in the integration of visuohaptic information include the ventrally-located lateral occipital complex (LOC) and the dorsally-located intraparietal sulcus (IPS). The response properties of these regions are only beginning to be explored in children, and thus far, very little is known about the development of functional connectivity between the dorsal and ventral streams for supporting visuohaptic processing. Here, BOLD fMRI measurements from a block design experiment involving visual and haptic exploration of real objects and textures in three groups of participants (4 to 5.5 year olds, 7 to 8.5 year olds, and adults) were used to examine the development of task-dependent functional connectivity between the LOC and the IPS. General psychophysiological interaction (gPPI) methods of analysis were implemented to measure the strength of functional connections between these neural substrates across experimental conditions. Results showed greater functional connectivity from the LOC seed region-of-interest (ROI) to bilateral caudal IPS in 4 to 5.5 year olds as compared to 7 to 8.5 year olds and adults during haptic, but not visual, processing. Correspondingly, functional connectivity from the IPS seed ROI to the LOC during haptics was also greater

in young children compared to older children and adults. These findings indicate strong bidirectional functional connections between the dorsal and ventral streams early on, but a gradual uncoupling of these sensory processing streams with development, a result that is consistent with multisensory developmental perceptual narrowing of these sensory systems. Importantly, a transition period occurs between 4 and 8 years of age during which the neural substrates supporting haptics become uncoupled, possibly to allow for the fine-tuning of other perceptual systems (e.g., vision) later in development.

4.1. Introduction

Vision and haptics are arguably two of the most salient sensory modalities used to support interactions with the environment and the objects within it. One of the key characteristics of objects that is shared across these two modalities involves geometric properties, or shape information (Amedi et al., 2007; James et al., 2002b; Stilla and Sathian, 2008). The integration of vision and haptics allows us to process three-dimensional shape quickly and efficiently for object recognition, including object perception and object-directed action. There is strong evidence that the underlying organization of visual, haptic, and visuohaptic object processing is separated into two different, but interactive, streams within the brain (e.g., James, Kim, & Fisher, 2007; Kim & James, 2010).

One of the dominant theories concerning the way in which the visual stream is organized is the two visual streams theory. According to this theory, the dorsal and ventral streams process the same sensory information for different purposes (Goodale & Milner, 1992; Ungerleider & Mishkin, 1982). While visual control of object-directed

actions is mediated by the dorsal visual stream, perceptual object recognition is mediated by the ventral visual stream (Goodale and Milner, 1992; Milner and Goodale, 1995). As an extension of this theory, and combining visual and haptic object processing, James and colleagues (2007) proposed a model in which multisensory shape cues for planning object-directed motor actions are processed at the convergence of the dorsal visual and haptic pathways at the intraparietal sulcus (IPS), and multisensory shape information for object perception is processed at the convergence of the ventral visual and haptic pathways at the lateral occipital complex (LOC). A plethora of studies has now substantiated this model; visuohaptic shape processing has been found consistently to recruit a subregion within the LOC, often labeled as lateral occipital tactile-visual (LOtv; Amedi et al., 2001, 2002, 2005; Jao, James, & James, 2014; James et al., 2002a, 2002b; James & Kim, 2010; James, Kim, & Fisher, 2007; Stilla & Sathian, 2008), as well as the anterior, medial, and caudal aspects of the IPS (Binkofski et al., 1999; Bodegard et al., 2001; Culham & Kanwisher, 2001; Grefkes et al., 2002; Jao, James, & James, 2014; James et al., 2002a; James & Kim, 2010; James, Kim, & Fisher, 2007; Peltier et al., 2007; Roland, O'Sullivan, & Kawashima, 1998; Stilla & Sathian, 2008; Zhang et al., 2004). The separation of these visuohaptic regions within the dorsal and ventral streams in adults may allow multisensory information to be processed efficiently for object perception versus object-directed action. Although there is some evidence of interactions between these streams in adults (see Peltier et al., 2007; Sathian et al., 2011), it remains unknown how the two streams interact in children to support multisensory object recognition.

Developmentally, the neural response properties of the ventral LOC and dorsal IPS are only beginning to be explored in children. There is currently a paucity of

neuroimaging studies examining these neural substrates during object recognition, and the majority of this research has focused on the visual domain only (Dekker et al., 2011; Golarai et al., 2007; Scherf et al., 2007). While some studies have found visual activity in the LOC and IPS to be adult-like sometime between 5 to 8 years of age, few have examined the development of haptic or visuohaptic substrates. In one particular study testing children aged 4 to 5.5 years, 7 to 8.5 years, and adults during visuohaptic object recognition, findings showed that the neural substrates implicated in adults, including the LOC and IPS, were involved in children at an early age (Jao, James, & James, 2014). The development of these regions, however, was protracted compared to primarily visual or haptic substrates, possibly due to the greater complexity involved in integrating visuohaptic information. Moreover, the activation patterns in these regions were not yet adult-like by 8 years for simple object perception tasks. In a related study on older children from 7 to 8.5 years and adults during crossmodal tasks, findings showed similar patterns of neural activity across the two groups in these regions, although activity was once again weaker in the children (Jao, James, & James, under review). Thus, while the dorsal (IPS) and ventral (LOC) neural substrates supporting multisensory object recognition appear to be active early on, they are still undergoing development depending on the functional task. These results may be caused by underlying shifts in the patterns of functional connectivity between the dorsal and ventral streams across development; these shifts can be captured by examining task-dependent functional connectivity.

Because the brain is a highly complex network of interconnected regions (Sporns, 2012), task-based functional connectivity measures can provide a clearer picture of the developmental progression of the brain's circuitry that is used for object recognition.

Specifically, general psychophysiological interaction (gPPI) methods of analysis on developmental fMRI data can be used to determine how multisensory neural regions in the dorsal and ventral streams change in terms of functional connectivity across different age groups. In brief, this method estimates the functional coupling, or strength of synchronous activity, between a pre-selected seed region-of-interest (ROI) and the rest of the brain during specific psychological tasks (Friston et al., 1997; McLaren et al., 2012; O'Reilly et al., 2012; Neufang et al., 2008). Regions that indicate strong correlations imply greater functional, context-dependent connectivity (McLaren et al., 2012).

Different measures have been used to investigate the networks involved in multisensory object recognition in adults. Previous research examining effective connectivity during haptic object shape perception has implicated a bidirectional and covarying interaction between the LOC and multisensory aspects of the IPS, as well as between other motor and somatosensory regions (Deshpande et al., 2008; Lacey, Stilla, Sreenivasan et al., 2014). While these studies investigated task-related connectivity only in adults, it nevertheless provides support for known multisensory convergence areas as being highly interconnected regions that are well-correlated during perceptual recognition tasks. As of yet, the development of functional connectivity between the dorsal and ventral regions and other cortical areas for supporting visuohaptic object processing remains unknown. Therefore, the current study examined the developmental changes in functional connectivity during visual and haptic processing to address how the connections between visuohaptic areas (particularly the LOC and IPS), as well as other regions in the brain, change across development.

Several sets of mutually exclusive hypotheses and predictions are possible. In

terms of multisensory systems, one of the key developmental theories of sensory perception is perceptual narrowing. This theory suggests that the initial broad tuning of multisensory signals may in fact narrow over time with selective sensory experience (for a review, see Lewkowicz and Ghazanfar (2009)). Based on this notion, it is hypothesized that (1) the strength of functional connectivity between dorsal and ventral visuohaptic systems may decrease w/ increasing age. That is, as children become older and gain more experience with visuohaptic object processing for object perception versus object-directed actions, it is predicted that the sensory systems will perhaps become more specialized to support efficient processing of multisensory information. Alternatively, (2) functional connectivity between the dorsal and ventral regions may increase over time, suggesting that development is progressive. According to the progressive theories of development, basic perceptual abilities gradually emerge and are increasingly refined with experience (Wallace, 2004). It is also conceivable, however, that there may be no change in functional connections between the dorsal and ventral streams, but instead, there may be changes in the strength of functional connectivity between multisensory regions and earlier, unisensory areas. Based on behavioral studies, both unisensory vision and haptics appear to be adult-like by 5 years (Bushnell & Baxt, 1999; Kalagher & Jones, 2011). Yet, neuroimaging studies indicate that although vision and haptics are fairly well-developed, they arguably are not yet adult-like by 5 years for some types of object recognition (Golarai et al., 2007; Scherf et al., 2007; Jao, James, & James, 2014). Thus, it is possible that (3) the functional connections between specific unisensory cortices and multisensory cortices may increase with development to support multisensory integration as they become more adult-like. Conversely, (4) functional connections may decrease

with development due to perceptual narrowing. Finally, (5) there may be no changes in functional connectivity across the different age groups, which would suggest that synchronous activation patterns between neural regions for object recognition are adult-like early on by 4 years of age.

4.2. Methods

For the following subsections: *4.2.1. Participants, 4.2.2. Stimuli, 4.2.3. Neuroimaging procedure, and 4.2.4. MRI data acquisition and preprocessing*, please refer to sections *2.1* to *2.4* of Jao, James, & James (2014). Briefly, functional magnetic resonance imaging (fMRI) was used to measure the blood oxygen level dependent (BOLD) response in three groups of participants (4 to 5.5 year olds, 7 to 8.5 year olds, and adults). The task consisted of blocked visual and haptic exploration of real objects and textures, which yielded four conditions: visual objects (VO), visual textures (VT), haptic objects (HO), and haptic textures (HT). A general psychophysiological interaction (gPPI) analysis of functional connectivity (see Friston et al., 1997; McLaren et al., 2012) was used on the previously collected BOLD fMRI data described in Jao, James, & James (2014) to measure the strength of synchronous activity between visuohaptic neural substrates in the current study.

4.2.5. Data analysis procedures

4.2.5.1. General psychophysiological interaction (gPPI) method of analysis

Functional data were analyzed using the general form of PPI to determine the functional synchrony between seed regions-of-interest and other cortical areas (Friston et al., 1997; McLaren et al., 2012). This method included three types of regressors: (1) the variables

of the experimental paradigm (i.e., psychological predictors); (2) the measurements of neural activity within a specific cortical seed region (i.e., physiological predictors); and (3) the interaction between the first two predictors (i.e., psychophysiological interactions).

Psychological predictors in the design matrix were based on the presentation timing of the blocked stimuli, and were comprised of the four conditions (VO, HO, VT, and HT). These predictors were convolved with a two-gamma impulse response function. Six motion parameters including three translation and three rotation parameters along the *x*, *y*, and *z* axes were also included as predictors of no interest and thresholded at 5 mm on all axes; any functional runs with motion estimates exceeding this threshold were excluded. Although this is more liberal than in previous adult studies, it was implemented here because a stricter criterion would have removed many of the child participants (see Supplementary materials in Jao, James, & James (2014)). In addition to standard motion correction, time series censoring was performed on motion spikes, which were also included as predictors of no interest.

For each individual participant, whole-brain statistical parametric maps (SPMs) were calculated using fixed-effects general linear models (GLMs) and a conjunction contrast of visual objects versus visual textures and haptic objects versus haptic textures (i.e., (VO > VT) ∩ (HO > HT)). This contrast was used to functionally define multisensory visuohaptic object-selective regions in each hemisphere, including the lateral occipital complex (LOC) and the intraparietal sulcus (IPS) indicated by previous studies (Amedi et al., 2001, 2002, 2005; James et al., 2002b; James & Kim, 2010; Stilla & Sathian, 2008), to be used as seed ROIs in the gPPI analysis. Activity was evoked in

the LOC for 32 out of 36 participants, and in the IPS for 33 out of 36 participants. The participants whose seed ROIs could not be localized using this contrast were solely from the group of 4 to 5.5 year olds, and their data were discarded from further analyses. The neural responses (i.e., beta weights) from each seed ROI were then extracted and input in separate gPPI models as the physiological predictors. Results showed similar patterns between hemispheres, and as previous studies have shown robust effects in the left hemisphere (Kim & James, 2010; Kim, Stevenson, & James, 2012), we present data from the left seed ROIs for convenience (see Fig. 1 for individual seeds).

The four psychological predictors (as well as the "censor" predictors of no interest, which may have contributed to the neural signal) were multiplied with the physiological predictor to form the interaction terms for each participant. The gPPI predictors from this third type of regressor were entered into separate random-effects GLMs, one for each seed region. A 2x2x3 design matrix was input in the BrainVoyager QX^{TM} 2.4 ANCOVA module with BOLD signal change (beta weights) as the dependent variable, stimulus type (objects and textures) and sensory modality (vision and haptics) as the within-subjects factors, and age group (4 to 5.5 year olds, 7 to 8.5 year olds, and adults) as the between-subjects factor. Whole-brain SPMs were calculated using the GLMs by applying contrasts that were thresholded with a minimum voxel-wise *p*-value of $< .01$ per map, and corrected for multiple testing with a cluster threshold of at least 61 contiguous 1x1x1 mm voxels. This threshold was determined by Monte Carlo simulation using the BrainVoyager QX^{TM} Cluster-size Estimation Plug-in, which estimates the cluster-size threshold required to produce an alpha-level of $< .05$ based on a specific voxel-wise *p*-value.

4.2.5.2. Post-hoc Region-of-Interest analysis

A post-hoc Region-of-Interest (ROI) analysis was performed to examine the strength of functional connections directly between the functionally-defined multisensory LOC and IPS seed regions. The gPPI beta weights from the source seed region to the target seed region were extracted from each individual, and then averaged across each group for comparison. This analysis revealed no significant effects.

4.2.5.3. Motion tolerance threshold analyses

To rule out the possibility of motion driving any differences in neural activation between groups, motion tolerance threshold analyses were implemented (for a detailed description of these analyses, see Supplementary materials in Jao, James, and James (2014)). Within each group, mean motion was compared to the BOLD signal change extracted from: 1) the seed-to-seed functional connections (described above), and 2) the regions showing significant group differences in functional connectivity from the left LOC seed as revealed by the whole-brain maps. Results showed that the correlation between mean motion and the seed-to-seed BOLD signals was not significant in any of the groups (4 to 5.5 year olds: ($r^2(8) = 0.105$, p = n.s.); 7 to 8.5 year olds: ($r^2(11) = 0.003$, p = n.s.); adults: ($r^2(6) = 0.002$, p = n.s.); overall: ($r^2(29) = 0.023$, p = n.s.)). Similarly, the correlation between mean motion and BOLD signals from regions showing group differences was not significant in any group (4 to 5.5 year olds: ($r^2(9) = 0.035$, p = n.s).; 7 to 8.5 year olds: ($r^2(11) = 0.077$, p = n.s.); adults: ($r^2(6) = 0.036$, p = n.s.); overall: ($r^2(30) = 0.047$, p = n.s.)). Therefore, it is unlikely that group differences in the strength of functional connections are driven by head motion.

4.3. Results

Several whole-brain contrasts were performed to assess the development of the functional connections between visuohaptic regions in the dorsal and ventral streams. Importantly, the developmental changes in task-dependent functional connectivity were measured by examining group differences in connection strength from the seed ROIs to the rest of the brain. Statistical Parametric Maps (SPMs) revealed strong functional connections from the left IPS and LOC seed regions to areas in the dorsal and ventral streams, as well as to other cortical areas (Table 1). These effects, however, were significantly greater only when comparing 4 to 5.5 year olds to the 7 to 8.5 year olds and adults (i.e., (4 to 5.5 yo > 7 to 8.5 yo + Adults)); the older children and adults showed no significant whole-brain group differences.

4.3.1. HO + HT

Whole-brain results for haptic processing (HO + HT) showed functional connections in terms of task-dependent synchrony from the ventral to dorsal streams, that is, between the ventrally-located left LOC seed ROI and the dorsally-located bilateral caudal IPS (Fig. 2A, green circles). Additionally, functional connections were present within the ventral stream from the left LOC to the right LOC (Fig. 2A, white circles), and were stronger in 4 to 5.5 year olds as compared to 7 to 8.5 year olds and adults.

Correspondingly, there was a functional connection from the dorsal to ventral stream, specifically between the dorsally-located left IPS seed ROI and the ventrally-located left LOC during haptic processing. This was also stronger in 4 to 5.5 year olds as compared to the 7 to 8.5 year olds and adults (Fig. 2B, white circles). Both seed ROIs showed further functional connections to bilateral frontal areas (Fig. 2A-B, right axial slices;

Table 1). The two older groups demonstrated similar connection strengths overall for haptics.

4.3.2. VO + VT

For visual processing (VO + VT), results indicated no significant differences between the age groups in the patterns of functional connectivity from either the left LOC or the left IPS seed region. Synchronous task-based functional activity from the two visuohaptic processing centers to the rest of the brain appeared to be similar across the three age groups for processing visual object and texture stimuli.

4.3.3. HO > VO

Results from the whole-brain contrast comparing haptic to visual object processing (HO > VO) showed a functional connection from the LOC seed ROI to the primary visual cortex (V1) and surrounding extrastriate areas (Fig. 3). This task-dependent connection was stronger in the younger children than in the older children and adults; the older two groups did not show this effect.

4.4. Discussion

The neural substrates supporting adult visuohaptic object processing are well known, and include regions in the dorsal and ventral streams such as the IPS and the LOC, respectively (Amedi et al., 2001, 2005; James & Kim, 2010; James, Kim, & Fisher, 2007; Stilla & Sathian, 2008). In children, we have previously shown that the neural resources allocated to vision and haptics change with increased sensory experience over time and highly depend on the type of stimuli and task (Jao, James, & James, 2014; Jao, James, & James, under review). To our knowledge, however, this is the first study to implement gPPI analyses in the investigation of functional connections underlying visuohaptic

processing, and the first to examine these changes developmentally. The results of the current study showed strong bidirectional functional connections between the dorsal and ventral streams that decreased with age. Further results demonstrated functional connections within the ventral visual stream for haptic object processing, suggesting early crosstalk between the visual and haptic systems. These, too, decreased with age. Together, the findings provide evidence for dorsal and ventral stream uncoupling that occurs with haptic development. Moreover, they reveal a process of multisensory perceptual narrowing of sensory regions wherein the initially broad multisensory tuning of visual areas becomes narrower with development.

4.4.1. Dorsal and ventral stream uncoupling

The multisensory seed ROIs showed strong bidirectional functional connections in terms of correlation strength between the LOC and IPS during haptic object and texture processing. These effects were significantly greater in young children as compared to older children and adults, indicating a decrease in functional synchrony between regions within the dorsal and ventral streams that occurred with increasing age. These findings suggest strong functional connections between the dorsal and ventral streams early on, but a gradual uncoupling of the sensory processing streams with development. This is in accordance with our first hypothesis: while the separation of visuohaptic systems in children eventually leads to adult-like efficiency in processing sensory information for perception versus action (see James and Kim (2010)), the dorsal and ventral streams may be highly interconnected (particularly in support of haptic processing) in young children because they do not yet have sufficient multisensory experience for adult-like specialization of these two systems. Indeed, previous behavioral studies have shown that

while unisensory haptic object recognition is fairly stable by 5 years, crossmodal visuohaptic recognition abilities are not (Bushnell & Baxt, 1999). Moreover, the integration of visuohaptic shape information does not become statistically optimal until after 8 years of age, suggesting that there is a lack of efficiency in combining sensory information prior to this age (Gori et al., 2008). Combined, these behavioral findings implicate an underdeveloped neural system supporting visuohaptic object recognition in young children. The systems underlying haptic processing may be less differentiated—and therefore more coupled—in the 4 to 5.5 year olds, which is reflected here by their strong functional connections between the dorsal and ventral streams.

The functional connections between the dorsal and ventral streams during visual object and texture processing, however, did not differ between groups. This provides evidence that the functional connections supporting vision are in place by 4 years of age, and do not change drastically with development. As such, the "long-range" functional connections between visuohaptic regions in the dorsal and ventral streams for visual processing appear to be adult-like in young children. Nevertheless, this does not preclude the possibility of the fine-tuning of some forms of visual processing, which may continue on a local neuronal scale. In particular, prior research examining the development of the LOC has shown that this region is generally recruited for visual object recognition between 5 to 8 years of age (Dekker et al., 2011; Golarai et al., 2007; Grill-Spector, Golarai, & Gabrieli, 2008; Scherf et al., 2007), although visual object preference and crossmodal recognition continue to increase with age (Jao, James, & James, 2014; Jao, James, & James, under review). Behavioral findings have also indicated that the recognition of more complex forms such as faces and objects from unusual views is

protracted compared to simple shapes (Bova et al., 2007; Juttner et al., 2006; Mondloch et al., 2003; Mondloch, Le Grand, & Maurer, 2002; Mondloch, Maurer, & Ahola, 2006), which suggests a delayed development of the occipitotemporal cortex (see Jao, James, and James (under review)). Thus, while the developmental trajectory within visuohaptic regions such as the LOC may be protracted, the development of functional connections across these regions in support of visual processing is fairly adult-like early on.

The seed regions were targeted as multisensory object-selective areas within the LOC (i.e., the LOtv; see Amedi et al. (2005)) and the IPS. Based on the whole-brain gPPI results, it appeared that these regions within the dorsal and ventral streams were functionally linked to one another in 4 to 5.5 year olds. Although it is possible that the functional connections between the two streams involved the visuohaptic subregions within the IPS and LOC, it is also conceivable that these functional connections formed a link between multisensory and unisensory subregions. To disentangle these possibilities, a seed-to-seed ROI analysis was implemented based on each individual's set of seed regions. This analysis revealed that while aspects of the LOC and IPS were functionally connected to one another (for similar connections found via effective connectivity, see Deshpande et al. (2008) and Lacey et al. (2014)), the visuohaptic subregions within the seeds were not. Thus, the dorsal and ventral streams were connected in a very specific manner in which the visuohaptic subregion of IPS was not connected to the visuohaptic subregion of the LOC, and vice versa. This may imply that visual and haptic unisensory information follow different channels that link to the multisensory subregions.

4.4.2. Multisensory perceptual narrowing

In the development of visuohaptic functional connectivity networks, the LOC correlated

not only with the IPS, but also with nearby unisensory areas. Specifically, regions within the ventral stream and putative visual cortex, including the LOC and primary visual cortex (V1), were highly functionally connected during haptic processing in young children, but not in older children or adults. This is partially in accordance with our fourth hypothesis in which the strength of functional connectivity between the visuohaptic LOC and an earlier unisensory area decreased with development. Contrary to this prediction, however, there were also changes in functional connections between the dorsal and ventral streams (see subsection *4.4.1. Dorsal and ventral stream uncoupling*). These results suggest extensive crosstalk between the visual and haptic systems early on that decreases with age, and are consistent with the developmental theory of multisensory perceptual narrowing (for a review, see Lewkowicz and Ghazanfar (2009)). Particularly, it seems to be the case that as children age and gain more experience with visuohaptic object perception, the two sensory systems, which are initially very coupled, begin to specialize based on their selective experience. The visual and haptic systems become more narrowly tuned, and thus follow a regressive rather than a progressive process (Lewkowicz & Ghazanfar, 2009). Sometime between 4 and 8 years of age, a transition period occurs during which the neural substrates in the visual cortex (as well as in the dorsal and ventral streams) that support haptic perception become uncoupled, possibly to allow for the fine-tuning of other perceptual systems (such as vision, discussed in the previous subsection) later in development.

The pattern of results in children indicating activation of visual cortical areas during haptic perception is consistent with previous studies; there have been precedents of similar findings within adults. In particular, haptic shape processing has been found

frequently to recruit areas within the visual cortex such as the LOC (James & Kim, 2010; James, Kim, & Fisher, 2007; Stilla & Sathian, 2008; for reviews, see Lacey and Sathian (2014) and Amedi et al. (2005)). More recently, changes in haptic shape have been shown to recruit early visual areas along the visual pathway, suggesting that haptic shape perception may involve the entire ventral stream (Snow, Strother, & Humphreys, 2014). Nonetheless, it can be argued that these effects within the ventral stream were due to visual imagery. Several studies have demonstrated that visual imagery of haptically explored objects activates regions within the visual cortex (Lacey, Tal, Amedi, & Sathian, 2009; Lacey et al., 2014; Sathian et al., 1997). Yet, this is unlikely in the current study given that the contrast used to determine the functional connections within the ventral visual stream compared haptic objects to visual objects. While visual imagery during haptic perception may activate regions in the occipital cortex, this activation is not likely to be stronger than activation induced by visually perceiving the object.

The developmental decreases in functional connectivity between the LOC and V1, as well as between the LOC and IPS, during haptic perception appear to be due to multisensory perceptual narrowing. Yet, the uncoupling of these regions over time may be driven not only by changes in the development of visuohaptic processing and selective sensory experience, but also by an increasing emphasis on metamodal shape processing. According to the concept of a "metamodal" brain, the brain is organized not by discrete unisensory inputs, but rather by *task-specific* multisensory inputs (Amedi et al., 2007; James & Kim, 2010; Lacey et al., 2009; Pascual-Leone and Hamilton, 2001). This type of organization would allow information such as shape to be processed regardless of the input sensory modality. As both vision and haptics encode properties pertaining to object

shape quickly and efficiently, the two sensory modalities likely share overlapping neural substrates in the LOC and the IPS (James & Kim, 2010). Developmentally, there may be a shift in emphasis wherein less is placed on the specific sensory modality used to process object shape, and more is placed on the actual shape properties. Thus, the uncoupling of vision and haptics, and of the dorsal and ventral streams, may follow a developmental trajectory that simultaneously involves regressive sensory changes due to multisensory perceptual narrowing, as well as a shift to metamodal (shape) information processing. Further research, however, is needed to substantiate this notion.

4.4.3. Unexpected findings, considerations, and concerns

4.4.3.1. Unexpected frontal functional connections

Across the left seed ROIs, the results revealed dense functional connections from the LOC and IPS to bilateral frontal regions in the 4 to 5.5 year olds as compared to the 7 to 8.5 year olds and adults. These unexpected findings suggest that there is greater communication between the frontal cortex and the dorsal and ventral streams during haptic processing in young children. While fairly little is currently known about the neural mechanisms underlying visuohaptic object processing in children, what is known stems primarily from adult neuroimaging studies. These have suggested that haptic shape processing occurs in dorsal frontoparietal areas including the IPS, precentral gyrus, anterior insular cortex, and middle frontal gyrus (Snow, Strother, & Humphreys, 2014), as well as in the occipitotemporal cortex and the LOC (Amedi et al., 2002, 2005; James, James, Humphrey, & Goodale, 2005; James & Kim, 2010; James, Kim, & Fisher, 2007; Lacey et al., 2009). Yet, even in adults, it is unknown how multisensory regions within the dorsal and ventral streams functionally connect to the specific areas shown in the

present study to support haptic shape processing (although see Deshpande, Hu, Lacey, Stilla, and Sathian (2010), and Lacey, Stilla, Sreenivasan, Deshpande, and Sathian (2014)). Although we could speculate and offer reverse inferences as to why these functional connections are so prevalent in young children and not in older children or adults for haptics, the current study was not designed to address these particular differences in frontal functional connections. Thus, these effects clearly warrant further investigation.

4.4.3.2. Motion considerations

One salient concern in developmental neuroimaging is motion. It is a fact that young children produce more in-scanner head motion than older children or adults, and this motion can influence the neural signal, resulting in spurious effects (Davidson, Thomas, & Casey, 2003; Poldrack, Pare-Blagoev, & Grant, 2002; Thomas & Casey, 2003). To ameliorate any motion effects in the data, several precautions were taken including standard offline motion correction algorithms that added 3D motion predictors of no interest to be regressed, as well as additional time point censoring of motion spikes as predictors of no interest. This ensured that activity driven by motion was removed from the initial model. In implementing the gPPI analysis, the "censor" predictors, which may have contributed to the physiological signal, were also used as interaction terms with the physiological predictor and were included as predictors of no interest in the PPI model. Post-hoc correlations comparing mean motion (see Supplementary material in Jao, James, and James (2014)) to both the between-seed effects, as well as the whole-brain group effects, revealed no significant findings. Combined, these methods and tests provide support for our lack of seed-to-seed connections, and more importantly, for our functional

connectivity effects as not due to motion artifacts.

4.4.3.3. Variability of individual seed ROIs

Another concern in developmental neuroimaging is the potential variability in selecting individual functional seed ROIs across developmental age groups, and the effect on the neural results. Many studies have indicated that children show lower and more diffuse activity than adults (Casey, Galvan, & Hare, 2005; Durston et al., 2006; Stiles, Moses, Passarotti, Dick, & Buxton, 2003; although, see Brown, Petersen, and Schlaggar (2006)). This diffusivity could be attributed to less overlap between individual ROIs in children as compared to adults, rather than to an actual decrease in BOLD signal. Indeed, our previous findings demonstrated greater variability of individual ROIs in young children (Jao, James, & James, 2014). In that study, the Euclidean distance from the prototypical mean center of mass (in mm) was calculated for each group and each region, and mean absolute distances from the prototypical center were used to determine the variability. The 4 to 5.5 year olds showed a greater spread or dispersion of seed ROIs than the 7 to 8.5 year olds or adults (see Fig. 1 for left seed locations). Based on our current results, however, this concern of ROI variability can be allayed. A greater dispersion of seed ROIs in young children should result in lower signals than in older children or adults who show a similar spread of ROIs; however, the findings demonstrate that it is the young children who show higher neural signals in terms of stronger functional connections than the two older groups. Therefore, the pattern of results cannot be due to variability in individual seed ROIs.

4.4.4. Conclusions

In summary, the neural patterns presented here from BOLD fMRI and gPPI suggest

decreases in bidirectional functional connectivity between the IPS and the LOC during haptic processing that occur with increasing age. As such, the findings indicate strong functional connections between the dorsal and ventral streams early on, but a gradual uncoupling of these sensory processing streams with development. Moreover, regions within the putative visual cortex, including the LOC and primary visual areas, were shown to be highly functionally connected in young children during haptic processing. This pattern was not present in older children or adults, suggesting multisensory perceptual narrowing of these sensory systems with development. Importantly, a transition period occurs between 4 and 8 years of age during which the neural substrates supporting haptics become uncoupled, possibly to allow for the fine-tuning of other perceptual systems (such as vision) later in development.

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Table 1. Clusters of functional connections by seed ROI and contrast for 4 to 5.5 yo > 7 to 8.5 yo + Adults. Talairach coordinates (*x*, *y*, *z*), peak *t*-values, *p*-values, and number of voxels are provided for each cluster (L = left; R = right; LOC = lateral occipital complex; IPS = intraparietal sulcus; MFG = middle frontal gyrus; STG = superior temporal gyrus; AIC = anterior insular cortex).

Region		*x*	*y*	*z*	*t*-value	*p*-value	No. of Voxels
L LOC Seed					*t*(31)		
(HO + HT)							
	R LOC	44	-65	3	4.032	.0003	1973
	L caudal IPS	-19	-68	42	3.685	.0009	2348
	R caudal IPS	11	-59	33	4.595	.0001	4124
	L MFG	-22	-5	48	4.485	.0001	2958
	R MFG	23	1	45	5.220	.0000	2441
	R MFG	47	22	24	4.414	.0001	1928
	L paracingulate	-10	-8	60	4.280	.0002	1980
	R paracingulate	14	-5	60	4.440	.0001	2197
	R STG	53	-44	15	4.555	.0001	3653
	R precentral gyrus	50	-8	36	4.558	.0001	4103
(HO > VO)							
	V1	5	-77	12	3.759	.0007	3872
L IPS Seed					*t*(32)		
(HO + HT)							
	L LOC	-40	-59	-6	4.502	.0001	3783
	L lingual gyrus	-16	-62	0	4.072	.0002	1996
	L AIC	-46	7	15	4.364	.0001	3101
	R AIC	29	16	18	3.927	.0004	1556
	L MFG	-31	16	33	4.602	.0001	1430
	R MFG	25	14	34	3.774	.0007	784

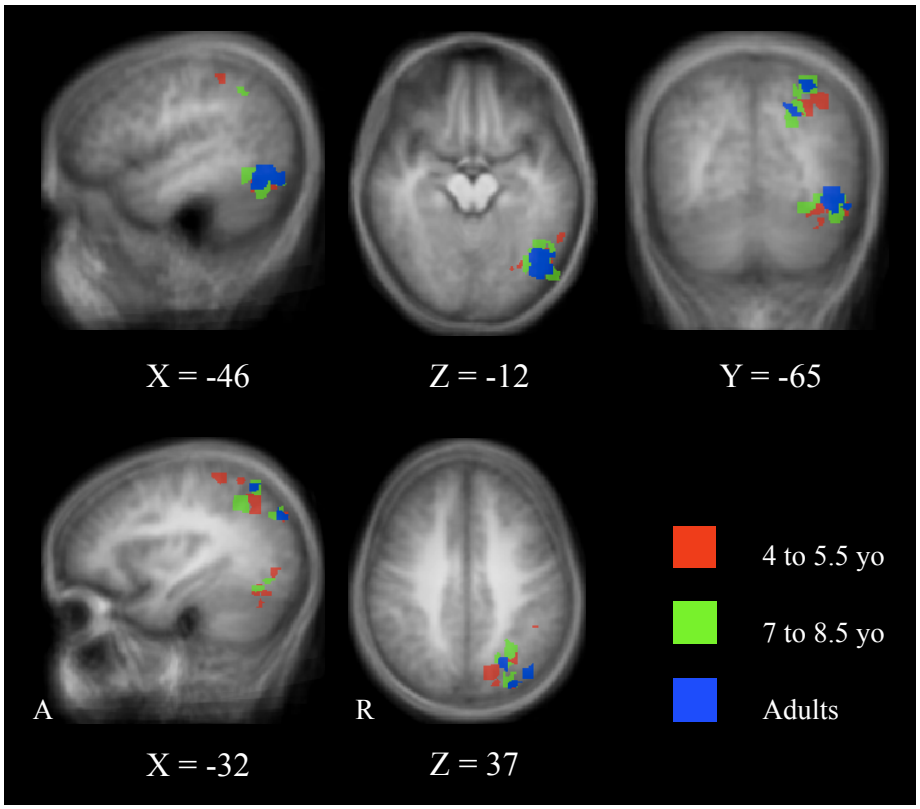

Figure 1. Individual seed ROIs. Colored regions on averaged human brain maps show the locations of each individual's left seed ROIs (LOC and IPS) within the three age groups. Red represents the 4 to 5.5 year old children, green represents the 7 to 8.5 year old children, and blue represents the adults (A = anterior; R = right).

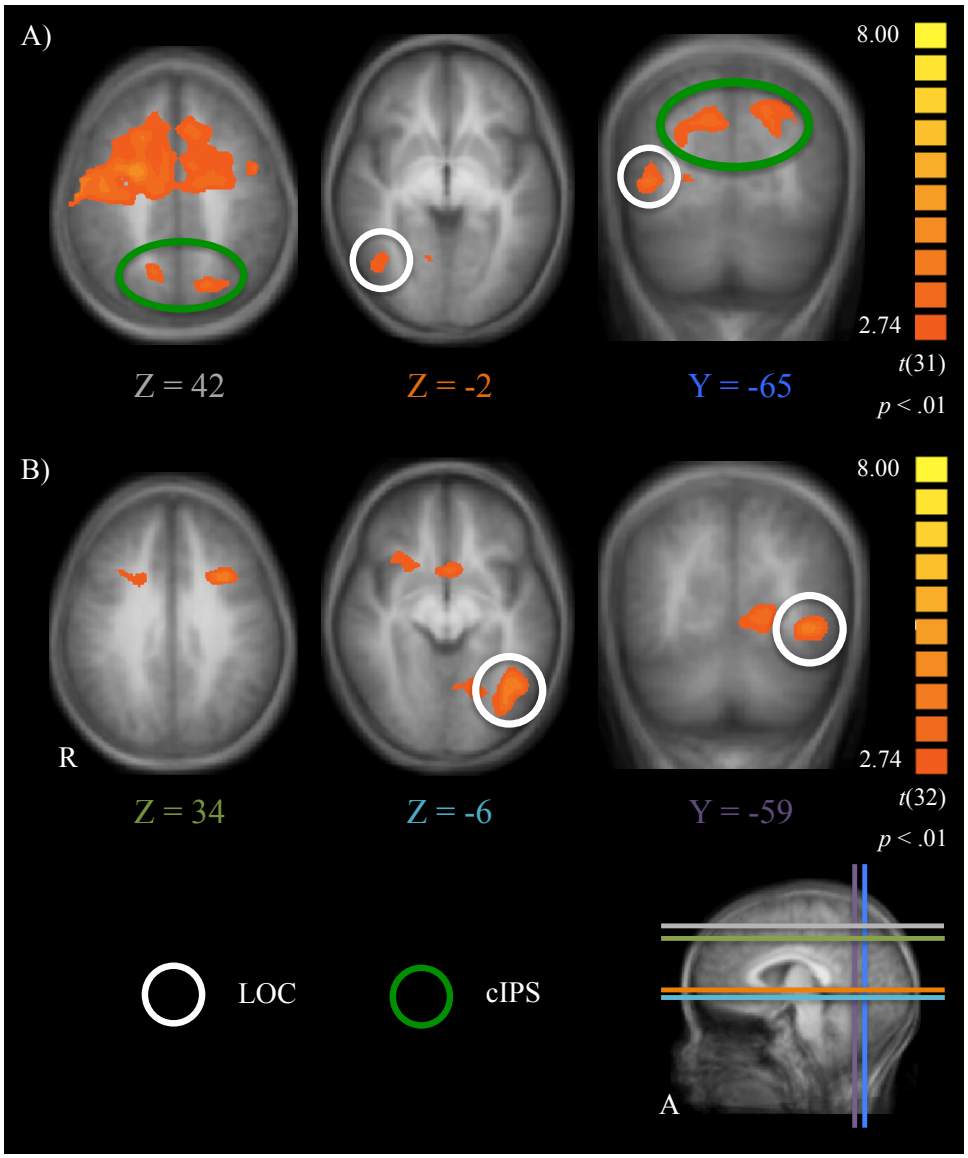

Figure 2. Functional connections from the seeds for haptic processing. Statistical parametric maps (SPMs) of task-dependent functional connectivity between: A) the left LOC seed ROI and the whole brain, and B) the left IPS seed ROI and the whole brain using a balanced contrast of HO + HT in 4 to 5.5 yo > 7 to 8.5 yo + Adults. Colors on the coronal and axial slices correspond to lines on the sagittal slice. On this and subsequent figures, data are presented on an averaged human brain, and corrected for multiple comparisons with a voxel-wise threshold of $p < .01$ (LOC = lateral occipital complex; cIPS = caudal intraparietal sulcus; ROI = region of interest).

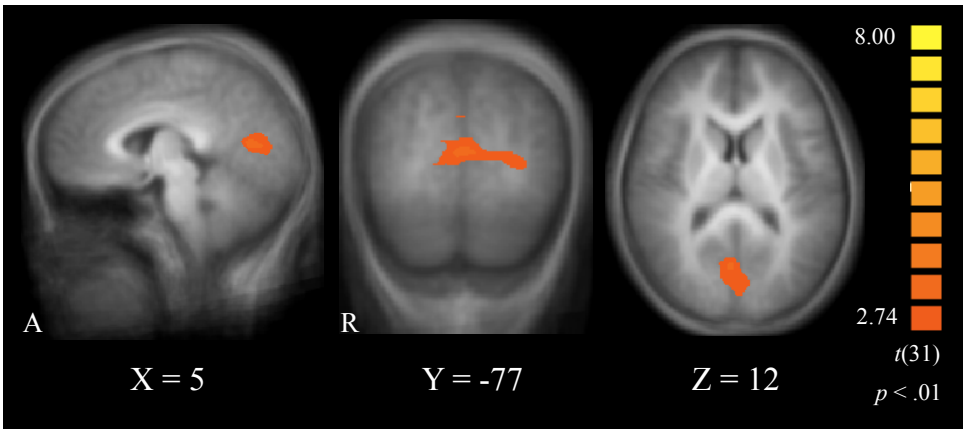

Figure 3. Functional connections from the left LOC seed for haptic versus visual objects. SPMs of task-dependent functional connectivity between the left LOC seed and the whole brain using a balanced contrast of HO > VO in 4 to 5.5 yo > 7 to 8.5 yo + Adults.

Chapter 5.

General Discussion

5.1. Overview

Object recognition is ubiquitous and essential for interacting with the surrounding multisensory environment. The sensory inputs from vision and haptics converge quickly and efficiently to guide this interaction, particularly with regard to the geometrical (i.e., shape) properties of objects for recognition and perception. The systems supporting visuohaptic object recognition in the brain are well-studied in adults, however, there is currently a paucity of research surrounding the neural development of haptic and visuohaptic processing in children. Thus, the primary research goal of the present work was to understand the neural development of multisensory visuohaptic processing. Two specific aims were addressed: 1) to investigate how the neural mechanisms involved in visuohaptic object recognition develop; and 2) to determine how the visuohaptic systems interact in the brain and change over time. This dissertation spanned from the initial mapping of individual visual and haptic sensory systems in young children, to the examination of those areas for evidence of multisensory convergence and crossmodal sharing of visual and haptic information, and finally, to the investigation of the functional connections between those regions.

5.2. Summary of studies

In Chapter 2, the neural mechanisms underlying visuohaptic object recognition were investigated in children from 4 to 5.5 years, 7 to 8.5 years, and adults. This functional

magnetic resonance imaging (fMRI) study outlined the developmental trajectories of the lateral occipital complex (LOC) and the intraparietal sulcus (IPS) for visual and haptic convergence of object shape information – these trajectories were previously unknown in children. The findings indicated that object preference became increasingly visually dominant with age, while haptic object preference remained fairly stable early on. Importantly, the development of visuohaptic neural substrates for object recognition was protracted compared to unisensory substrates.

In Chapter 3, the neural correlates of crossmodal processing were examined using a delayed match-to-sample task with novel objects in children aged 7 to 8.5 years and adults. Results showed crossmodal enhancement in the LOC, suggesting that this region was sensitive to changes in sensory modality on a neuronal level. Critically, although this effect, as well as the network of multisensory regions consistently found in adults, was present in children by 7 years with similar patterns of activation as adults, neural activity was more widespread during sample encoding and weaker in signal during test matching in children as compared to adults. This indicated ongoing development of crossmodal processing in children through 7 years of age.

In Chapter 4, the changes in functional connectivity during visuohaptic object processing in children aged 4 to 5.5 years and 7 to 8.5 years and in adults were explored using general psychophysiological interaction (gPPI) methods of analysis. Results demonstrated strong functional connections between the dorsal and ventral streams early on for haptic processing, but an uncoupling of these sensory processing streams with development. Functional connectivity between the two visuohaptic convergence areas for visual processing, however, was similar across age, suggesting that the connections

supporting basic visual abilities were in place by 4 to 5.5 years. These findings indicated multisensory perceptual narrowing of visuohaptic processing areas with specific sensory experience over development.

5.3. Developmental trajectory of visuohaptic object processing

The findings from these studies have implications for an overarching developmental trajectory of visuohaptic object processing that combines aspects from several theories underlying the development of multisensory perception (see subsection *1.5.4. Developmental theories for multisensory perception*). In accordance with the dynamic systems approach, developmental changes occurred via complex interactions among multiple sensory systems with differing levels of stability (Thelen & Smith, 1994). The development of visuohaptic processing was supported by interactions within each of the visual and haptic systems, as well as across these sensory systems (for a conceptual diagram of the developmental changes by age group, see Fig. 1). Visually, object preference increased in the LOC and IPS over time, while functional connections between these regions were stable. Haptically, object preference remained stable in the LOC and IPS, while the functional connections between them uncoupled with age. Visuohaptically, multisensory processing was protracted compared to unisensory processing, and crossmodal recognition also increased in the LOC. Together, these patterns showed developmental changes in the interactions between visuohaptic systems interspersed with varying levels of stability. This suggests that the development of visuohaptic object recognition is a dynamic process that involves a highly adaptive interplay between the sensory systems.

The patterns also reflected a regressive process of multisensory perceptual narrowing (Lewkowics & Ghazanfar, 2009). According to this theory, as children gain experience with visuohaptic object processing, the two sensory systems, which are initially very coupled, begin to specialize and become more narrowly tuned. This was indeed demonstrated by the broad functional connections between the dorsal and ventral streams (as well as within the ventral visual stream) in young children during haptic processing that decreased with age. As such, the uncoupling of the LOC and IPS for haptics, in conjunction with stable functional connectivity between these regions for vision, implicated a narrowing of visuohaptic substrates perhaps to allow the fine-tuning of perceptual processes (e.g., crossmodal recognition) to continue on a neuronal level.

Taken together, these studies indicate that the development of visuohaptic object recognition cannot be described as a unitary process that follows a linear and progressive trajectory. It rather involves dynamic interactions between several distinct systems that are, at times, regressive, and that follow different developmental timelines throughout childhood and into adulthood (Fig. 1). Crucially, the complexity of sensory inputs and perceptual tasks impacts the development of visuohaptic neural substrates including the dorsally-located IPS and the ventrally-located LOC. The more complicated and abstract forms of multisensory and crossmodal object processing show protracted developmental trajectories as compared to the processing of simple, unimodal shapes, which appears to be adult-like at a fairly young age (e.g., Grill-Spector, Golorai, & Gabrieli, 2008; Scherf et al., 2007). Furthermore, the weakening over time of functional connectivity between visuohaptic areas during haptic processing may facilitate tuning within other perceptual systems, such as vision, that occurs later in development. Thus, the development of

visuohaptic object processing follows a nonlinear trajectory involving multiple highly interactive systems, each of which proceeds along a different developmental timeline.

5.4. Limitations and future directions

One of the primary limitations of this body of work concerns the determination of areal versus neuronal convergence of visual and haptic signals within known multisensory areas (see subsection *1.5.1. Definitions of "multisensory"*). Although the results from Chapter 2 provided developmental trajectories of the LOC and IPS in children for visuohaptic object processing using fMRI, these findings were limited to interpretations regarding areal convergence. Yet, areal and neuronal convergence are not mutually exclusive. A wealth of data from the subsequent crossmodal study described in Chapter 3 suggested that further fine-tuning of these systems for visuohaptic convergence may occur on a neuronal level. These findings demonstrated crossmodal enhancement during test matching within the LOC, which necessarily involved communication between sensory neurons from the sample encoding to test matching phases. This study therefore provided strong support for multisensory convergence at a neuronal level.

Future studies may target neuronal convergence of visual and haptic signals more directly. Specifically, a multisensory visuohaptic condition may be added to examine neuronal convergence within the LOC and IPS via superadditivity or subadditivity metrics (i.e., the sum of neural activation produced by unisensory conditions is greater or less than that produced by the multisensory condition, which would indicate differential processing of sensory stimuli by unisensory versus multisensory neurons; Beauchamp, 2005a, 2005b; Laurienti et al., 2005). A manipulation of salience, or signal-to-noise ratio,

along with unisensory and multisensory conditions may also be implemented to measure neuronal convergence through inverse effectiveness—an inverse relationship wherein decreasing stimulus effectiveness produces increased multisensory enhancement (Holmes 2007, 2009; James & Kim, 2010; Kim, Stevenson, & James, 2012; Meredith and Stein, 1986). That is, as stimuli are degraded, they become less effective at stimulating sensory neurons; this in turn drives increases in multisensory gain. These methods would offer more in-depth knowledge regarding the development of visuohaptic processing in the LOC and IPS in children, and combined with crossmodal paradigms, would allow for stronger interpretations of multisensory convergence on a neuronal level.

The changes in functional connections supporting crossmodal visuohaptic processing can also be examined in future studies. This would elucidate the connectivity patterns between the LOC and IPS during more complex forms of multisensory processing, as well as any further developmental interactions between the dorsal and ventral streams. Lastly, the present work binned development into three very specific age groups based on previously reported transition periods of sensory processing abilities. While the age groups were targeted in this work for their behavioral capabilities, clearly testing a wider gamut of age ranges would be useful for providing a detailed account of the more subtle neural changes across development.

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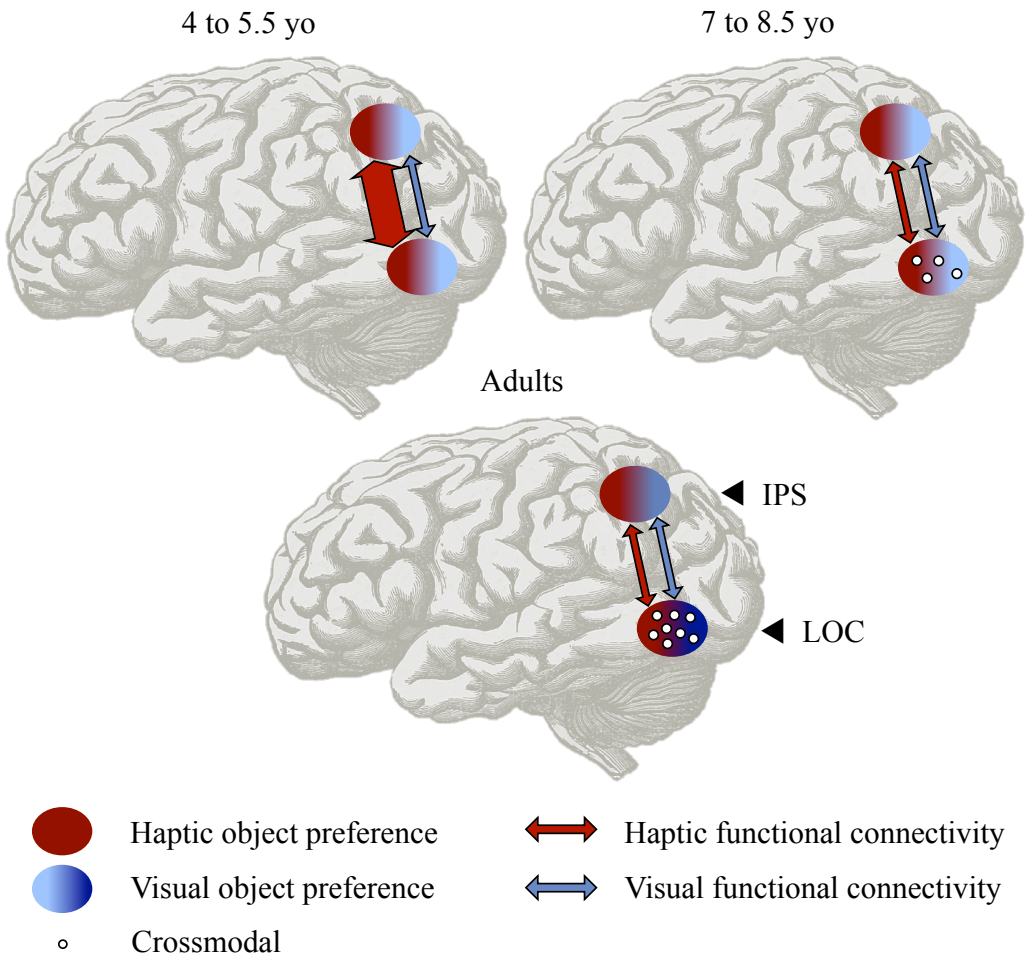

Figure 1. Developmental trajectory of visuohaptic object processing in the LOC and IPS. Conceptual diagram of the developmental changes in haptic and visual object preference, haptic and visual functional connectivity, and crossmodal processing in children from 4 to 5.5 years and 7 to 8.5 years and in adults. Darker colors, thicker arrows, and larger number of dots represent greater neural activity/functional connectivity.

Ruth Joanne Jao

Address: Dept. of Psychological and Brain Sciences, Indiana University
1101 E 10th St. Bloomington, IN 47405
Lab Phone: 812.856.1926 • Email: rjjao@indiana.edu

Education:

Doctoral Candidate pursuing a joint Ph.D. in:
Cognitive Science
Psychological and Brain Sciences
Concentration: *Cognitive Neuroscience*
Dissertation Title: *The Neural Development of Visuohaptic Object Processing*
Indiana University (IU), Bloomington, IN
Graduation: May, 2015 Cumulative GPA: 3.93/4.00

Bachelor of Science, Cognitive Science
Bachelor of Arts, Philosophy
Minor: Dance
University of California San Diego (UCSD), La Jolla, CA
Graduated: June, 2009 Cumulative GPA: 3.78/4.00
Honors/Awards: Magna Cum Laude
Phi Beta Kappa 2008
Provost's Honors
Departmental Honors in Cognitive Science

Honors and Awards:

- NSF IGERT Travel Award Summer, 2015
- IU Women in Science Provost Travel Award Summer, 2015
- NSF IGERT Travel Award Summer, 2014
- IU Women in Science Provost Travel Award Summer, 2013
- NSF Graduate Research Fellowship Program: Honorable Mention 2012
- NSF IGERT Training Grant 2011 – 2013
- IU McFall Summer Research Award Summer, 2011
- NIH Developmental Training Grant 2010 – 2011
- IU Graduate Women in Science Award 2010
- UCSD Chancellor's Research Scholarship Summer, 2008

Research Interests:

Functional neuroimaging; Functional connectivity; Sensorimotor learning; Visuohaptic perception; Multisensory integration; Object recognition; Cognitive and perceptual development.

Research Experience:

Perception and Neuroimaging Lab **(Thomas W. James)** – Graduate Student 05/2013 – Present
IU, Cognitive Science Program, Dept. of Psychological and Brain Sciences – Bloomington, IN

- Examined human multisensory visual and haptic perception for object processing

- Implemented functional neuroimaging (fMRI), functional connectivity (PPI), behavioral, and modeling methods and analyses
- Mentored undergraduate research assistants

Cognition and Action Neuroimaging Lab **(Karin H. James)** – Graduate Student 08/2010 – Present
IU, Cognitive Science Program, Dept. of Psychological and Brain Sciences – Bloomington, IN
- Investigated development of multisensory integration and crossmodal processes
- Created and analyzed fMRI and behavioral experiments for children and adults

Movement Control Lab **(Emanuel Todorov)** – Research Scientist 10/2009 – 08/2010
Univ. of Washington, Dept. of Computer Science and Engineering – Seattle, WA
- Studied human motor control via (active; passive) Motion Capture and EMG
- Created psychophysics experiments to examine sensorimotor control, learning, and adaptation in complex, dynamical systems
- Performed statistical data analyses and modeling
- Implemented Matlab for stimulus presentation and data recording

Interactive Cognition Lab **(David Kirsh)** – Lab Asst.; Student Research Asst. 01/2009 – 09/2009
UCSD, Dept. of Cognitive Science – La Jolla, CA
- Coded, annotated, and analyzed behavioral, survey, questionnaire, interview, and video data from human subjects (professional dancers) during sensorimotor processing, learning, and collective group interactions
- Prepared materials for presentations of research and data at conferences
- Performed system administration duties
- Implemented iRODs for confidential data storage onto servers at Calit2, UCSD

The Neurosciences Institute **(Aniruddh Patel)** – Research Asst. 07/2008 – 08/2010
NSI, Theoretical Neurobiology, Music and the Brain – La Jolla, CA
- Coded animal behavioral data (Snowball, *sulphur-crested cockatoo*)
- Catalogued and analyzed gesture vocabulary for dissemination of research on animal movement, rhythmic entrainment to auditory stimuli, and creativity

Cognitive Development Lab **(Gedeon Deak)** – Student Research Asst. 10/2007 – 08/2010
UCSD, Dept. of Cognitive Science – La Jolla, CA
- Studied longitudinal infant behavior to model the emergence of shared attention
- Examined the development of visuomotor skills and responses to social cues
- Developed questionnaire and video coding schemes, and analysis methodologies
- Trained lab members in coding and video analysis
- Honors Thesis: *Infant comprehension of visual obstruction and referential gaze following from 14 to 18 months*

Teaching Experience:

P211 – Methods of Experimental Psychology (Associate Instructor) Fall, 2013
IU, Dept. of Psychological and Brain Sciences – Bloomington, IN

P433 – Laboratory in Neuroimaging Methods (Teaching Assistant) Spring, 2014; Spring 2015
IU, Dept. of Psychological and Brain Sciences – Bloomington, IN

P335 – Cognitive Psychology (Teaching Assistant) Summer, 2014
IU, Dept. of Psychological and Brain Sciences – Bloomington, IN

P349 – Cognitive Neuroscience (Teaching Assistant) Fall, 2014
IU, Dept. of Psychological and Brain Sciences – Bloomington, IN

Guest Lectures:

P433 – Normalization and Coregistration; Functional Specialization 02/2015
P349 – Brain and Cognition 11/2014
P349 – Social Cognitive Neuroscience 11/2014
P349 – Higher Perceptual Functions 10/2014
P349 – Object Recognition 10/2014

Posters & Published Abstracts:

Jao, R. J., James, K. H., & James, T. W. (accepted). The development and organization of visuohaptic modality-biased signals in the LOC. 15th Annual Meeting of the Vision Sciences Society.

Jao, R. J., James, K. H., & James, T. W. (2014, July). Development of dorsal and ventral stream connectivity: A visuohaptic psychophysiological interaction study. Poster presented at the 1st Vision Science Expo at Indiana University. Bloomington, IN.

Jao, R. J., James, K. H., & James, T. W. (2014, May). Functional connectivity analysis shows developmental changes in visuohaptic brain networks. Poster presented at the 26th Association for Psychological Science Annual Convention, San Francisco, CA.

Jao, R. J., James, K. H., & James, T. W. (2014). Development of dorsal and ventral stream connectivity: A visuohaptic psychophysiological interaction study. *Journal of Vision, 14* (10), 1104; doi:10.1167/14.10.1104

Jao, R. J., James, K. H., & James, T. W. (2014, April). Developmental changes in functional connectivity: A visuohaptic psychophysiological interaction study. Poster presented at the 5th Annual IGERT Showcase at Indiana University. Bloomington, IN.

Jao, R. J., James, T. W., & James, K. H. (2013, October). Crossmodal visuohaptic recognition: A look at (and feel for) objects. Poster presented at the 3rd Indiana Neuroimaging Symposium at Indiana University. Bloomington, IN.

Jao, R. J., James, T. W., & James, K. H. (2013, October). The neural development of crossmodal processing as measured by fMRI. Poster presented at the Center of Excellence for Women in Technology Research and Technology Showcase at Indiana University. Bloomington, IN.

Jao, R. J., James, T. W., & James, K. H. (2013). Visuohaptic crossmodal matching: A developmental fMRI study. *Journal of Vision, 13* (9), 1330.

Jao, R. J., James, T. W., & James, K. H. (2013, April). Visuohaptic crossmodal matching: A developmental fMRI study. Poster presented at the 4th Annual IGERT Spring Research Showcase at Indiana University. Bloomington, IN.

Jao, R. J. & Deak, G. O. (2012, June). The development of referential gaze-following and perspective-taking from 14 to 18 months. Poster presented at the 18th Biennial International Conference on Infant Studies. Minneapolis, MN.

Jao, R. J., James, T. W., & James, K. H. (2012, April). Multisensory convergence of vision and haptics across development. Poster presented at the 19th Annual Meeting of the Cognitive Neuroscience Society. Chicago, IL.

Jao, R. J., James, T. W., & James, K. H. (2012, April). Multisensory convergence of vision and haptics across development. Poster presented at the 3rd Annual IGERT Spring Research Showcase at Indiana University. Bloomington, IN.

Jao, R. J. & Deak, G. O. (2010, August). Infant referential gaze following: When does intentionality begin? Poster presented at the 118th Annual Convention of the American Psychological Association. San Diego, CA.

Jao, R. J., Iversen, J. R., Patel, A. D., Bregman, M. R., & Schulz, I. (2010). Diverse movements in avian dancing to human music. In S. M. Demorest, S. J. Morrison, & P. S. Campbell (Eds.), *Proceedings of the 11th International Conference on Music Perception and Cognition* (p. 54). Adelaide: Causal Productions.

Jao, R. J. & Deak, G. O. (2009, October). Infant comprehension of visual obstruction and referential gaze following from 14- to 18-months. Poster presented at the Conference of Joint Attention: Developments in Philosophy of Mind, Developmental and Comparative Psychology, and Cognitive Science at Bentley University. Waltham, MA.

Peer-Reviewed Publications:

Jao, R. J., James, T. W., & James, K. H. (under review). Crossmodal enhancement in the LOC for visuohaptic object recognition over development.

Jao, R. J., James, K. H., & James, T. W. (in preparation). Developmental changes in visuohaptic functional connections between the dorsal and ventral streams.

Jao, R. J. & Deak, G. O. (in preparation). Seeing through obstructions: A longitudinal study of referential gaze following in 14 to 18 month olds.

Jao, R. J., Iverson, J. R., Patel, A. D., & Schulz, I. (in preparation). Avian movement repertoire and rhythmic entrainment.

James, K. H., Jao, R. J., & Berninger, V. (in press). The development of multi-leveled writing brain systems: Brain lessons for writing instruction. In MacArthur, C. A., Graham, S., & Fitzgerald, J. (Eds.), *Handbook of writing research*, 2nd edition. New York: Guilford.

Jao, R. J., James, T. W., & James, K. H. (2014). Multisensory convergence of visual and haptic object preference across development. *Neuropsychologia, 56*, 381-392.

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Kirsh, D., Muntanyola, D., Jao, R. J., Lew, A., & Sugihara, M. (2009). Choreographic methods for creating novel, high quality dance. *Proceedings of the 5th International Conference on Design and Semantics of Form and Movement* (pp. 188-195). Taipei, Taiwan.

Book Review:

Jao, R. J. (2008). [Review of the book *The Neurobehavioral and Social-Emotional Development of Infants and Children* by E. Tronick]. *Milton H. Erickson Foundation Newsletter*, *28*(3), 18.

Invited Talk (Conference):

Jao, R. J., James, K. H., & James, T. W. (2014, May). Development of visuohaptic functional connectivity. In T. W. James (Chair), Multisensory Convergence. Invited Symposium conducted at the 26th Association for Psychological Science Annual Convention. San Francisco, CA.

Presentations:

Jao, R. J., James, T. W., & James, K. H. (2012, November). A developmental fMRI look at (and feel for) crossmodal processing. Presentation at the Indiana University Developmental Seminar. Bloomington, IN.

Jao, R. J., James, T. W., & James, K. H. (2011, January). Multisensory convergence of vision and haptics across development. Presentation at the Indiana University Neuroimaging Group Seminar. Bloomington, IN.

Jao, R. J., Kalagher, H., James, T. W., Jones, S. S., & James, K. H. (2010, October). Multisensory Integration of vision and haptics across development. Presentation at the Indiana University Developmental Seminar. Bloomington, IN.

Jao, R. J. (2010, August). Infant referential gaze following and intentionality. Symposium presentation at the 118th Annual Convention of the American Psychological Association. San Diego, CA.

Jao, R. J. (2009, June). Infant comprehension of visual obstruction and referential gaze following from 14- to 18-months [Honors Thesis]. Paper presented at the Cognitive Science Undergraduate Honors Thesis Presentations at UCSD. San Diego, CA.

Jao, R. J. (2009, April). Infant comprehension of visual obstruction and referential gaze following from 14- to 18-months. Paper presented at the 22nd Annual Undergraduate Research Conference at UCSD. San Diego, CA.

Professional Organizations and Conference Memberships:

• Vision Sciences Society	2013 – 2015
• Association for Psychological Science	2014
• Cognitive Neuroscience Society	2012
• American Psychological Association	2010
• Cognitive Science Society	2010
• International Conference on Music Perception and Cognition	2010
• Temporal Dynamics of Learning Center (UCSD)	2008 – 2009

Coursework:

- Advanced Statistics in Psychology
- Brain and Cognition
- Cortical Control of Human Movement
- Developmental Cognitive Neuroscience
- Embodied Approaches to the Development of Brain and Behavior
- Embodied Cognitive Science
- Math and Logic for Cognitive Science
- Models in Cognitive Science
- Networks of the Brain
- Neural Science – Molecular Neuroscience
- Neural Science – Systems and Cognitive Neuroscience
- Neuroimaging Theory and Methods
- Neurophysiological Techniques
- Philosophical Foundations of Cognitive and Information Science
- Teaching of Psychology

Skills and Qualifications:

Statistics & programming
- SPSS, Excel, Matlab, R

Neuroimaging
- Functional Magnetic Resonance Imaging (fMRI)
- Functional connectivity (PPI – Psychophysiological Interactions)
- Data collection, preprocessing, and analysis in BrainVoyager QX™
- Sequential, crossmodal, and simultaneous presentations of visual and haptic stimuli
- IU Imaging Research Facility trained Level 1 MR personnel

Experimental design
- Matlab, SuperLab
- Visual and haptic presentations of object and texture stimuli
- Double Factorial Paradigm and Systems Factorial Technology for assessing cognitive processing mechanisms for multiple sources of information
- Behavioral experiments on sensorimotor control and learning, visuomotor development and joint attention, movement diversity in a non-human animal, and social collaborations for creativity

Subject populations
- Infants aged 3 to 24 months (behavior)
- Children aged 4 to 10 years (neuroimaging and behavior)
- Adults (neuroimaging and behavior)
- Professional dancers (behavior)
- Sulphur-crested cockatoo (behavior)

Additional skills
- Diverse background in research methodology and design for laboratory and field environments
- Extensive experience working with a variety of human subject populations
- Applied knowledge of statistical analyses of human subject data
- Proficiency in Mac OS, Windows, Linux, Microsoft Office
- Experience with grant writing/editing, IRB human subjects applications
- Motion capture (active: Phase Space; passive: Vicon) data collection, analysis, and modeling
- Electromyography data collection

Research Trainees:

• Grant Callen, Cox Research Scholar - B.S. Neuroscience, B.S. Psychology, 2015	2014 – 2015
• Rachel Crum - B.S. Neuroscience, 2017	2014 – 2015
• Rachel Winchell - B.S. Neuroscience, B.A. Psychology, 2011	2011 – 2012
• Laura Wright - B.S. Neuroscience, 2012	2011 – 2012
• Anna Bogun - B.A. Biochemistry, B.S. Neuroscience, 2011	2010 – 2011
• Heidi Treacy - B.A. Human Dev. & Family Studies, B.A. Psychology, 2011	2010 – 2011

Service:

- South Central Indiana Regional Science Fair Judge 2014 – 2015
- Ad-hoc reviewer for *Neuropsychologia*